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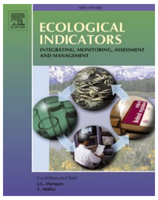

Review

Invasive alien species as reservoirs for pathogens

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ABSTRACT

Alien plant and animal hosts play an important role as vectors of dangerous pathogens. However, the knowledge on pathogens of many host species is still limited. To bridge this gap, we collated information on pathogens carried by 118 alien species in Europe in their native and secondary range. In Europe, these species are considered as invasive. Using the dataset we determined most prevailing pathogen groups and plant and animal hosts that carried the highest number of pathogens.

The most numerous pathogens were bacteria *Xylella fastidiosa* (plants) and Rabies virus (animals). The principal pathogen groups among plant hosts were Arthropoda (phylum), Insecta (class) and Hemiptera (order), and among animal hosts – Platyhelminthes (phylum), Trematoda (class) and Plagiorchiida/Strongylida (order). In plants, the highest number of pathogens was recorded for *Ambrosia artemisiifolia*; in animals, *Procyon lotor* was the most infested species. Hosts introduced from North America carried the highest numbers of pathogen species; in addition, unintentionally introduced hosts carried more pathogens than those introduced intentionally. We revealed also that the level of infestation differs between the habitats in which the hosts occur.

It should be also stressed that in all analyses the number of pathogens increased with the number of publications on the particular host' infestation. The highest number of publications was available for species useful for human, such as *Crassostrea gigas*. The results demonstrated that there are still significant gaps in the knowledge on the role of other hosts, including invasive ones (e.g., *Sciurus niger*) in pathogen transmission.

1. Introduction

While wild animals have always been regarded as the source of dangerous zoonoses (Kruse et al., 2004) and European wild plants together with many house and garden plants contain chemical substances that lead to toxic effects in animals (Anadón et al., 2018), the role of alien species as a factor increasing the risk of disease outbreaks has not been fully acknowledged yet (Blackburn and Ewen, 2017). The particular position of alien species as a risk factor comes from the fact that their introduction into a new area often results in co-introduction of new pathogens, not previously present there (Lymbery et al., 2014). Some of those pathogens may then infest and severely threaten naïve local flora, fauna or/and humans – a mechanism known as pathogen spillover (Alexander et al., 2018; Becker et al., 2019). Conversely, alien species may also become infested with local pathogens, already present in the area of introduction, which is known as pathogen spillback (Fagre et al., 2021; Kelly et al., 2009). Such novel combinations may significantly modify local host-pathogen dynamics, leading for instance to an increase in pathogen abundance, and consequently, to exacerbating threats that they have previously posed.

Severe pathogen-related consequences of alien species presence are usually associated with a scenario in which populations of alien hosts are well-established, large and widely spread. However, there are examples of pathogen spillover even if alien hosts do not establish in new areas and their presence in the environment is transient. Although records of such “true exotics” often attract significant attention from the public and media, potential consequences of their short-term occurrence are often underestimated in scientific discourse, and consequently, in frameworks aiming at reducing the threat from invasive alien species (Solarz and Najberek, 2017).

The recent COVID-19 pandemics, caused by the outbreak of the novel coronavirus SARS-CoV-2, proven to be of animal origin, raised

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significant concerns about the role of wildlife trade in spread of pathogens (Mori et al., 2020; Rabalski et al., 2021). The risk resulting from unpredictability of such events is amplified by the fact that there are basic knowledge gaps in taxonomy of pathogens, their origins and potential or primary hosts (Roy et al., 2017). Although it is known that some hosts, such as primates or bats, play particularly important role as vectors of dangerous pathogens (Cui et al., 2019; Letko et al., 2020; Melaun et al., 2014), the knowledge is still far from being complete even with respect to health of humans, farmed animals or cultivated plants (Can et al., 2019; Estrada-Peña et al., 2014). When it comes to pathogens of wild animals and plants, the knowledge gaps are even more evident (Chinchio et al., 2020; Han et al., 2016; Hulme, 2014).

To partly bridge this gap, we assessed pathogens and parasites carried by 118 invasive alien plant and animal species (60 plants and 58 animals), majority of which are regulated under the European and Polish national legislature. We determined most prevailing pathogen groups and most infested host groups. This will help to prioritize efforts to reduce the threat of epidemiological threat caused by invasive plants and animals.

2. Methods

The selected host species (Table 1) and the used methodology were an essential part of the Harmonia^{+PL} procedure (General Directorate for Environmental Protection, 2019), carried out for negative impact risk assessment for invasive alien species in Poland.

The pool of the assessed species included 60 plants and 58 animals (Table 1). Animal hosts species represented 4 different phyla and covered 41 vertebrates, 10 arthropods, 6 molluscs and 1 ctenophore, while all plant hosts were vascular plants. Regarding the legal status, 19 of the assessed species were included both in the EU IAS Regulation (European Commission, 2017) and in the national Polish law on IAS (Decree, 2011), 29 were regulated only by the EU Regulation, and 32 – only by the national Polish law. The remaining 37 species were not included in either the above mentioned legal acts, yet they were identified as invasive alien by Polish General Directorate for Environmental Protection.

A comprehensive review of Online sources was carried out in December 2017 – February 2018 to collect data on pathogens, parasites and their vectors (e.g., aphid *Aphis fabae* – a vector for more than 30 plant pathogenic viruses; Fried et al., 2013) carried by the assessed species. If the Online data was only fragmentary or inconclusive, a thorough search of the cited references was carried out.

The following sources of information were used (numbers in brackets correspond to the total number of records on specific host-pathogen associations found in a given source):

CABI Invasive Species Compendium https://www.cabi.org/isc/ (1203).
NOBANIS – European Network on Invasive Alien Species https://www.nobanis.org/fact-sheets/ (124).
Centers for Disease Control and Prevention https://www.cdc.gov (92).
EPPO Global Database https://gd.eppo.int/ (82).
Invasive Species in Belgium http://ias.biodiversity.be/species/risk (44).
GB non-native species secretariat http://www.nonnativespecies.org/index.cfm?pageid=143 (40).
DAISIE - Inventory of alien invasive species in Europe http://www.europe-aliens.org (currently available at https://www.gbif.org/dataset/39f36f10-559b-427f-8c86-2d28afff68ca#citation) (24).
GISD – Global Invasive Species Database http://www.iucngisd.org/gisd (8).
Alien Species in Poland http://www.iop.krakow.pl/ias (2).

The data was collected not only from Europe but also from other areas, including native range of the assessed host species. In many cases, while describing harmful organisms, the original information sources did not differentiate between pathogens, parasites or diseases *sensu scricte* and other organisms that could, in this way or another, adversely affect the hosts. They included, for instance, vectors carrying pathogens, or herbivore insects. We extracted and analysed information of all those harmful organisms and we collectively refer to them as pathogens. Moreover, origin of recorded pathogens was not assessed in the collected dataset because in most of cases there was no data in this respect. Integrated Taxonomic Information System ITIS www.itis.gov was the main reference used to unify classification of the recorded cellular pathogens, and the World Register of Marine Species WORMS (www.marinespecies.org) and MycoBank (www.mycobank.org) were auxiliary references for taxa that were not represented in the ITIS. With a few exceptions, viruses were classified according to the ICTV Master Species developed by the International Committee on Taxonomy of Viruses (ICTV, 2019). Original pathogen names retrieved from the surveyed data sources are presented in supplementary Tables S1 and S2.

In a quarter of the retrieved records pathogens were identified only to the level of genus, family or order. In the two latter cases they were not included in the final dataset. For pathogens identified to the genus, we followed the original source to indicate whether a given record referred to one (sp.) or more (spp.) species. Such records were included in the list of pathogens carried by a given host in case when they were the only representatives of a respective genus in that host. In cases when more than 1 record of an unidentified congener pathogens were found in the same host (e.g., 3 records of *Borrelia* sp.), only 1 record was included in its pathogen list. However, if the same host was infested with a pathogen identified to the species level and with an unidentified pathogen belonging to the same genus (e.g., *Borrelia burgdorferi* and *Borrelia* sp.), both records were included, basing on an assumption that it is more likely that they represent two different pathogen species, rather than the same one. A more conservative approach was applied in statistical analyses – they were based exclusively on pathogens identified to the species level.

For each host species we determined its native range (at the resolution of continents), environment (terrestrial/freshwater/marine) and the prevailing mode of introductions (intentional/unintentional); for species not yet introduced into Europe mode of introduction is potential. These variables were used in statistical analyses of infestation of different taxonomic groups of the studied hosts. The analysis of plant hosts was carried out at the level of family, while taxonomic differences in animals were analysed at the level of class.

Moreover, to account for the level of knowledge on the assessed host species in the statistical analyses, the number of scientific papers published in 1945–2020 timespan was checked through the Web of Science (www.webofknowledge.com; access date 23.09.2020; Table 1). Basic Search function was used, with the Web of Science Core Collection as the selected database and Topic as the selected search field; the following search string was used as the search criterion: “Latin species name” and (“pathogen” or “parasite”).

2.1. Statistical analyses

The data were analyzed in R v. 4.0.3 and RStudio v. 1.4.1103 (R Development Core Team, 2015) with the use of the generalized linear models (GLM). All models assumed a Poisson distribution of the target variables. Within-factor comparisons were conducted using default R treatment contrasts. The reference groups in particular models were changed using *relevel* command. The results were plotted using ‘jtools’ and ‘interactions’ packages (Long, 2019, 2017).

Six models (3 for plants and 3 for animals) were created to determine the dominant pathogen phyla, classes and orders recorded on the hosts. The response variable was always the number of recorded pathogen species counted per the respective taxonomic group (phylum, class or

Table 1
The list of 118 alien host species assessed in the study, with basic information on taxonomy, native range, environment and type of introduction. The number of publications on the species infestation, checked through the Web of Science database and the number of pathogen species retrieved from online data sources are also presented. All references for this information is included in Tables S1, S2, which also contain pathogens identified to higher taxonomic levels (e.g. genus); such records were not taken into consideration here. 'No data' – the species was not represented in any of the source databases; 0 – no pathogen records were found for the species.

Host type	Host Latin name	Author of the species name	Host English Name	Phylum	Class	Family	Native range	Environment	Typ of Introduction	Number of publications in Web of Science	Number of pathogen species in Online sources
PLANTS	Acer negundo	L.	Box elder	Tracheophyta	Magnoliopsida	Sapindaceae	N America	Terrestrial	Intentional	8	13
	Ailanthus altissima	(Mill.) Swingle	Tree of heaven	Tracheophyta	Magnoliopsida	Simaroubaceae	Asia	Terrestrial	Intentional	22	7
	Alternanthera philoxeroides	(Mart.) Griseb.	Alligator weed	Tracheophyta	Magnoliopsida	Amaranthaceae	S America	Terrestrial	Unintentional	18	11
	Ambrosia artemisiifolia	L.	Annual bur-sage	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Unintentional	24	28
	Amelanchier spicata	(Lam.) K. Koch	Dwarf service berry	Tracheophyta	Magnoliopsida	Rosaceae	N America	Terrestrial	Intentional	0	1
	Asclepias syriaca	L.	Broadleaf milkweed	Tracheophyta	Magnoliopsida	Apocynaceae	N America	Terrestrial	Intentional	22	13
	Aster novi-belgii	L.	New York aster	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Intentional	0	12
	Azolla filiculoides	Lam.	Mosquito fern	Tracheophyta	Magnoliopsida	Salviniaceae	N America	Freshwater	Intentional	3	6
	Baccharis halimifolia	L.	Tree groundsel	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Intentional	3	7
	Bidens frondosa	L.	Common beggar-ticks	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Intentional	3	1
	Bromus carinatus	Hook. & Arn.	California brome	Tracheophyta	Magnoliopsida	Poaceae	N America	Terrestrial	Intentional	3	3
	Cabomba caroliniana	Gray	Carolina fanwort	Tracheophyta	Magnoliopsida	Cabombaceae	N America/ S America	Freshwater	Intentional	1	No data
	Celastrus orbiculatus	Thunb.	Asiatic bittersweet	Tracheophyta	Magnoliopsida	Celastraceae	Asia	Terrestrial	Intentional	4	3
	Clematis vitalba	L.	Old man's beard	Tracheophyta	Magnoliopsida	Ranunculaceae	Europe/ Africa/Asia	Terrestrial	Intentional	7	10
	Cornus sericea	L.	Redosier dogwood	Tracheophyta	Magnoliopsida	Cornaceae	N America	Terrestrial	Intentional	1	11
	Crassula helmsii	(Kirk) Cockayne	Australian swamp stonecrop	Tracheophyta	Magnoliopsida	Crassulaceae	Australia	Freshwater	Intentional	1	No data
	Echinocystis lobata	(F. Michx.) Torr. & A. Gray	Wild cucumber	Tracheophyta	Magnoliopsida	Cucurbitaceae	N America	Terrestrial	Intentional	1	3
	Eichhornia crassipes	(Mart.) Solms	Water-hyacinth	Tracheophyta	Magnoliopsida	Pontederiaceae	S America	Freshwater	Intentional	61	3
	Elodea canadensis	Michx.	Canadian waterweed	Tracheophyta	Magnoliopsida	Hydrocharitaceae	N America	Freshwater	Intentional	4	No data
	Elodea nuttallii	(Planch.) H. St. John	Nuttall's waterweed	Tracheophyta	Magnoliopsida	Hydrocharitaceae	N America	Freshwater	Intentional	1	No data
	Eragrostis albensis	H. Scholz	Elbe love grass	Tracheophyta	Magnoliopsida	Poaceae	Unclear	Terrestrial	Unintentional	0	No data
	Fraxinus pennsylvanica	Marshall	Green ash	Tracheophyta	Magnoliopsida	Oleaceae	N America	Terrestrial	Intentional	8	8
	Gunnera tinctoria	(Molina) Mirb.	Chilean gunnera	Tracheophyta	Magnoliopsida	Gunneraceae	S America	Terrestrial	Intentional	0	0
	Helianthus tuberosus	L.	Woodland sunflower	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Intentional	18	18
	Heracleum mantegazzianum	Sommier & Levier	Giant hogweed	Tracheophyta	Magnoliopsida	Apiaceae	Asia	Terrestrial	Intentional	5	4
	Heracleum persicum	Fischer	Persian hogweed	Tracheophyta	Magnoliopsida	Apiaceae	Asia	Terrestrial	Unintentional	3	1
	Heracleum sosnowskyi	Manden.	Sosnowski's hogweed	Tracheophyta	Magnoliopsida	Apiaceae	Asia	Terrestrial	Intentional	4	3
	Hydrocotyle ranunculoides	L. f.	Floating pennyroyal	Tracheophyta	Magnoliopsida	Apiaceae	N America	Freshwater	Intentional	3	5
	Impatiens capensis	Meerb.	Orange touch-me-not	Tracheophyta	Magnoliopsida	Balsaminaceae	N America	Terrestrial	Intentional	13	3
		Royle		Tracheophyta	Magnoliopsida	Balsaminaceae	Asia	Terrestrial	Intentional	7	10

(*continued on next page*)

Table 1 (*continued*)

Host type	Host Latin name	Author of the species name	Host English Name	Phylum	Class	Family	Native range	Environment	Typ of Introduction	Number of publications in Web of Science	Number of pathogen species in Online sources
	Impatiens glandulifera		Purple jewelweed								
	Impatiens parviflora	DC.	Small-flower touch-me-not	Tracheophyta	Magnoliopsida	Balsaminaceae	Asia	Terrestrial	Unintentional	3	14
	Lagarosiphon major	(Ridley) Moss	Oxygen-weed	Tracheophyta	Magnoliopsida	Hydrocharitaceae	Africa	Freshwater	Intentional	0	1
	Ludwigia grandiflora	(Michx.) Greuter & Burdet	Large-flower primrose-willow	Tracheophyta	Magnoliopsida	Onagraceae	S America	Freshwater	Intentional	0	1
	Ludwigia peploides	(Kunth) P.H. Raven	Floating primrose	Tracheophyta	Magnoliopsida	Onagraceae	N America/ S America	Freshwater	Intentional	0	No data
	Lupinus polyphyllus	Lindl.	Garden lupin	Tracheophyta	Magnoliopsida	Fabaceae	N America	Terrestrial	Intentional	6	6
	Lysichiton americanus	Hultén and St. John	American skunk cabbage	Tracheophyta	Magnoliopsida	Araceae	N America	Terrestrial	Intentional	0	No data
	Microstegium vimineum	(Trin.) A. Camus	Japanese stiltgrass	Tracheophyta	Magnoliopsida	Poaceae	Asia	Terrestrial	Unintentional	9	5
	Mimulus guttatus	DC.	Seep-spring monkeyflower	Tracheophyta	Magnoliopsida	Scrophulariaceae	N America	Terrestrial	Intentional	23	1
	Myriophyllum aquaticum	(Vell.) Verdc.	Parrot feather	Tracheophyta	Magnoliopsida	Haloragaceae	S America	Freshwater	Intentional	3	3
	Myriophyllum heterophyllum	Michx.	Broadleaf water-milfoil	Tracheophyta	Magnoliopsida	Haloragaceae	N America	Freshwater	Intentional	1	No data
	Parthenium hysterophorus	L.	Santa Maria feverfew	Tracheophyta	Magnoliopsida	Asteraceae	N America/ S America	Terrestrial	Unintentional	35	19
	Parthenocissus inserta	(A.Kern.) Fritsch	False Virginia-creeper	Tracheophyta	Magnoliopsida	Vitaceae	N America	Terrestrial	Intentional	0	5
	Pennisetum setaceum	(Forssk.) Chiov.	Fountain grass	Tracheophyta	Magnoliopsida	Poaceae	Africa/Asia	Terrestrial	Intentional	1	1
	Persicaria perfoliata	(L.) H. Gross	Asiatic tearthumb	Tracheophyta	Magnoliopsida	Polygonaceae	Asia	Terrestrial	Unintentional	1	No data
	Prunus serotina	(Ehrh.) Borkh.	Black cherry	Tracheophyta	Magnoliopsida	Rosaceae	N America	Terrestrial	Intentional	48	27
	Pueraria montana	(Lour.) Merr	Kudzu	Tracheophyta	Magnoliopsida	Fabaceae	Asia	Terrestrial	Intentional	7	7
	Quercus rubra	L.	Northern red oak	Tracheophyta	Magnoliopsida	Fagaceae	N America	Terrestrial	Intentional	63	23
	Reynoutria japonica	Houtt.	Japanese knotweed	Tracheophyta	Magnoliopsida	Polygonaceae	Asia	Terrestrial	Intentional	12	14
	Reynoutria sachalinensis	(F. Schmidt) Nakai	Giant knotweed	Tracheophyta	Magnoliopsida	Polygonaceae	Asia	Terrestrial	Intentional	27	3
	Reynoutria × bohemica	Chrtek & Chrtkova	Japanese knotweed	Tracheophyta	Magnoliopsida	Polygonaceae	Asia	Terrestrial	Intentional	1	No data
	Robinia pseudoacacia	L.	Post locust	Tracheophyta	Magnoliopsida	Fabaceae	N America	Terrestrial	Intentional	31	23
	Rosa rugosa	Thunb.	Ramanas rose	Tracheophyta	Magnoliopsida	Rosaceae	Asia	Terrestrial	Intentional	8	23
	Rudbeckia laciniata	L.	Coneflower	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Intentional	0	1
	Solidago canadensis	L.	Canadian goldenrod	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Intentional	27	14
	Solidago gigantea	Aiton	Smooth goldenrod	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Intentional	15	19
	Solidago graminifolia	(L.) Elliott	Flat-topped goldenrod	Tracheophyta	Magnoliopsida	Asteraceae	N America	Terrestrial	Intentional	2	0
	Spartina anglica	C.E.Hubb	Common cordgrass	Tracheophyta	Magnoliopsida	Poaceae	Europe	Terrestrial	Intentional	4	2
	Spiraea tomentosa	L.	Steeplebush	Tracheophyta	Magnoliopsida	Rosaceae	N America	Terrestrial	Intentional	0	1
	Ulex europaeus	L.	Common gorse	Tracheophyta	Magnoliopsida	Fabaceae	Europe	Terrestrial	Intentional	54	7
	Xanthium albinum	(Widder) H. Scholz	Riverside Cocklebur	Tracheophyta	Magnoliopsida	Asteraceae	Unclear	Terrestrial	Unintentional	1	1

(*continued on next page*)

Table 1 (*continued*)

Host type	Host Latin name	Author of the species name	Host English Name	Phylum	Class	Family	Native range	Environment	Typ of Introduction	Number of publications in Web of Science	Number of pathogen species in Online sources
ANIMALS	Aix galericulata	(Linnaeus, 1758)	Mandarin duck	Chordata	Aves	Anatidae	Asia	Terrestrial/ Freshwater	Intentional	2	3
	Alopochen aegyptiacus	(Linnaeus, 1766)	Egyptian goose	Chordata	Aves	Anatidae	Africa	Terrestrial/ Freshwater	Intentional	1	3
	Ameiurus nebulosus	(Le Sueur, 1819)	Brown bullhead	Chordata	Teleostei	Ictaluridae	N America	Freshwater	Unintentional	11	14
	Arion distinctus	Mabille, 1868	Darkface arion	Mollusca	Gastropoda	Arionidae	Europe	Terrestrial	Unintentional	2	6
	Arion lusitanicus	Mabille, 1868	Iberian slug	Mollusca	Gastropoda	Arionidae	Europe	Terrestrial	Unintentional	15	10
	Axis axis	(Erxleben, 1777)	Chital	Chordata	Mammalia	Cervidae	Asia	Terrestrial	Intentional	10	17
	Bison bison	L.	American bison	Chordata	Mammalia	Bovidae	N America	Terrestrial	Intentional	108	59
	Branta canadensis	L. 1758	Canada goose	Chordata	Aves	Anatidae	N America	Terrestrial/ Freshwater	Intentional	50	24
	Callosciurus erythraeus	Pallas, 1779	Pallas's squirrel	Chordata	Mammalia	Sciuridae	Asia	Terrestrial	Intentional	11	14
	Castor canadensis	Kuhl, 1820	Canadian beaver	Chordata	Mammalia	Castoridae	N America	Terrestrial/ Freshwater	Intentional	12	5
	Cervus canadensis	Erxleben, 1777	American elk	Chordata	Mammalia	Cervidae	N America	Terrestrial	Intentional	20	18
	Cervus elaphus sibiricus	NULL	No data	Chordata	Mammalia	Cervidae	N America	Terrestrial	Intentional	0	17
	Cervus nippon	Temminck, 1838	Sika deer	Chordata	Mammalia	Cervidae	Asia	Terrestrial	Intentional	67	17
	Chelydra serpentina	Linnaeus, 1758	Snapping turtle	Chordata	Reptilia	Chelydridae	N America	Freshwater	Intentional	19	8
	Chrysemys picta	(Schneider, 1783)	Painted turtle	Chordata	Reptilia	Emydidae	N America	Freshwater	Intentional	16	3
	Corbicula fluminalis	(O.F. Müller, 1774)	Asiatic clam	Mollusca	Bivalvia	Cyrenidae	Asia	Freshwater	Intentional	0	6
	Corbicula fluminea	(O.F. Müller, 1774)	Asian clam	Mollusca	Bivalvia	Cyrenidae	Asia	Freshwater	Intentional	24	9
	Corvus splendens	Vieillot, 1817	House crow	Chordata	Aves	Corvidae	Asia	Terrestrial	Unintentional	8	19
	Crassostrea gigas	(Thunberg, 1793)	Pacific giant oyster	Mollusca	Bivalvia	Ostreidae	Asia	Marine	Intentional	806	26
	Cynops pyrrhogaster	(Boie, 1826)	Japanese fire-bellied newt	Chordata	Amphibia	Salamandridae	Asia	Terrestrial/ Freshwater	Intentional	4	2
	Eriocheir sinensis	Milne-Edwards, 1853	Chinese mitten crab	Arthropoda	Malacostraca	Varunidae	Asia	Marine	Unintentional	152	7
	Graptemys pseudogeographica	(Gray, 1831)	Mississippi map turtle	Chordata	Reptilia	Emydidae	N America	Freshwater	Intentional	3	2
	Harmonia axyridis	(Pallas, 1773)	Harlequin ladybird	Arthropoda	Insecta	Coccinellidae	Asia	Terrestrial	Intentional	75	22
	Herpestes javanicus	É. Geoffroy Saint-Hilaire, 1818	Small Asian mongoose	Chordata	Mammalia	Herpestidae	Asia	Terrestrial	Intentional	2	15
	Lithobates (Rana) catesbeianus	Shaw, 1802	American bullfrog	Chordata	Amphibia	Ranidae	N America	Terrestrial/ Freshwater	Intentional	190	46
	Mnemiopsis leidyi	L. Agassiz, 1865	Warty comb jelly	Ctenophora	Tentaculata	Bolinopsidae	N America	Marine	Unintentional	14	7
	Muntiacus reevesi	Ogilby, 1839	Reeves' muntjac	Chordata	Mammalia	Cervidae	Asia	Terrestrial	Intentional	4	3
	Myocastor coypus	Molina, 1782	Coypu	Chordata	Mammalia	Myocastoridae	S America	Terrestrial/ Freshwater	Intentional	30	25
	Nasua nasua	Linnaeus, 1766	South American Coati	Chordata	Mammalia	Procyonidae	Asia	Terrestrial	Intentional	37	19
	Neogobius fluviatilis	(Pallas, 1811)	Monkey goby	Chordata	Teleostei	Gobiidae	Asia	Freshwater	Unintentional	16	41
	Neogobius gymnotrachelus	(Kessler, 1857)	Racer goby	Chordata	Teleostei	Gobiidae	Asia	Freshwater	Unintentional	2	42
	Neogobius melanostomus	(Pallas, 1814)	Round goby	Chordata	Teleostei	Gobiidae	Asia	Freshwater	Unintentional	73	40
	Neovison vison	(Schreber, 1777)	American mink	Chordata	Mammalia	Mustelidae	N America		Intentional	54	80

(*continued on next page*)

Table 1 (*continued*)

Host type	Host Latin name	Author of the species name	Host English Name	Phylum	Class	Family	Native range	Environment	Typ of Introduction	Number of publications in Web of Science	Number of pathogen species in Online sources
								Terrestrial/ Freshwater			
	Nyctereutes procyonoides	Gray, 1834	Raccoon dog	Chordata	Mammalia	Canidae	Asia	Terrestrial	Unintentional	108	59
	Odocoileus virginianus	(Zimmermann, 1780)	White-tailed deer	Chordata	Mammalia	Cervidae	N America	Terrestrial	Intentional	344	52
	Ondatra zibethicus	Linnaeus, 1766	Muskrat	Chordata	Mammalia	Muridae	N America	Terrestrial/ Freshwater	Unintentional	24	32
	Orconectes limosus	(Rafinesque, 1817)	Striped crayfish	Arthropoda	Malacostraca	Cambaridae	N America	Freshwater	Intentional	46	1
	Orconectes rusticus	(Girard, 1852)	Rusty crayfish	Arthropoda	Malacostraca	Cambaridae	N America	Freshwater	Intentional	10	1
	Orconectes virilis	Hagen, 1870	Virile crayfish	Arthropoda	Malacostraca	Cambaridae	N America	Freshwater	Intentional	9	2
	Oryctolagus cuniculus	Linnaeus, 1758	Rabbit	Chordata	Mammalia	Leporidae	Europe/ Africa	Terrestrial	Intentional	266	72
	Oxyura jamaicensis	(Gmelin, 1789)	Ruddy duck	Chordata	Aves	Anatidae	N America	Terrestrial/ Freshwater	Intentional	1	1
	Pacifastacus leniusculus	(Dana, 1852)	American crayfish	Arthropoda	Malacostraca	Astacidae	N America	Freshwater	Intentional	162	3
	Perccottus glenii	Dybowski, 1877	Amur sleeper	Chordata	Teleostei	Odontobutidae	Asia	Freshwater	Unintentional	50	102
	Piaractus brachypomus	(Cuvier, 1818)	Pirapitinga	Chordata	Teleostei	Characidae	S America	Freshwater	Intentional	14	1
	Procambarus clarkii	Girard, 1852	Red swamp crayfish	Arthropoda	Malacostraca	Cambaridae	N America	Freshwater	Intentional	167	36
	Procambarus fallax f. virginalis	(Hagen, 1870)	No data	Arthropoda	Malacostraca	Cambaridae	N America	Freshwater	Intentional	13	1
	Procyon lotor	Linnaeus, 1758	Raccoon	Chordata	Mammalia	Procyonidae	N America	Terrestrial	Intentional	255	133
	Proterorhinus marmoratus	(Pallas, 1814)	Tubenose goby	Chordata	Teleostei	Gobiidae	Asia	Freshwater	Unintentional	15	38
	Pseudorasbora parva	(Schlegel, 1842)	Topmouth gudgeon	Chordata	Teleostei	Cyprinidae	Asia	Freshwater	Unintentional	46	69
	Psittacula krameri	(Scopoli 1769)	Ring-necked parakeet	Chordata	Aves	Psittacidae	Africa/Asia	Terrestrial	Intentional	11	5
	Rhithropanopeus harrisii	Gould, 1841	Dwarf crab	Arthropoda	Malacostraca	Panopeidae	N America	Marine	Unintentional	29	2
	Sciurus carolinensis	Gmelin, 1788	Grey squirrel	Chordata	Mammalia	Sciuridae	N America	Terrestrial	Intentional	42	50
	Sciurus niger	Linnaeus, 1758	Fox squirrel	Chordata	Mammalia	Sciuridae	N America	Terrestrial	Intentional	8	39
	Sinanodonta woodiana	(Lea, 1834)	Chinese pond mussel	Mollusca	Bivalvia	Unionidae	Asia	Freshwater	Unintentional	13	2
	Tamias sibiricus	Laxmann, 1769	Siberian chipmunk	Chordata	Mammalia	Sciuridae	Asia	Terrestrial	Intentional	16	20
	Threskiornis aethiopicus	(Latham, 1790)	Sacred ibis	Chordata	Aves	Threskiornithidae	Africa/Asia	Terrestrial	Intentional	2	5
	Trachemys scripta	Schoepff, 1792	Pond slider	Chordata	Reptilia	Emydidae	N America	Freshwater	Intentional	53	16
	Vespa velutina nigrithorax	de Buysson, 1905	Asian hornet	Arthropoda	Insecta	Vespidae	Asia	Terrestrial	Unintentional	1	6

order) and per host (collectively termed “the number of occurrences of pathogen species” here); it should be also noted that the Results section (in the text and at figures) includes also “unique species”, that is, the absolute number of pathogen species in the respective taxonomic groups, counted only once, regardless of the number of occurrences; this parameter was not included in statistical models. In all models, the pathogen taxonomic group was a single fixed effect. Pathogen groups represented only by a single pathogen group-host association were excluded from the GLM, because of lack of within-group variability. In plant phyla these were: Artverviricota, Mollusca, Blastocladiomycota; in plant classes: Alphaproteobacteria, Blastocladiomycetes, Duplopiviricetes, Gastropoda, Revtraviricetes, Secernentea, Tremellomycetes, Pezizomycetes; in plant orders: Architaenioglossa, Atheliales, Blastocladiales, Boletales, Dorylaimida, Durnavirales, Microascales, Myriangiales, Ophiostomatales, Ortervirales, Pezizales, Phyllachorales, Rhabditida, Rhizobiales, Santalales, Tremellales, Tymovirales, Urocystidales, Ustilaginales, Vibrionales, Xylariales. One fungal pathogen, *Ceratopycnis clematidis* (found in one host), cannot be unequivocally ascribed to any class or order, thus it was excluded from the respective GLMs (Table S1).

Similarly, in case of animal pathogens, there were pathogen groups associated only with a single host, and they were also excluded from the analyses. In animal phyla these were: Annelida, Basidiomycota, Blastocladiomycota, Cercozoa, Cnidaria, Fungi, Metamonada and Perkinsozoa; in classes: Anthozoa, Ascetosporea, Blastocladiomycetes, Copepoda, Entomophthoromycetes, Gastropoda, Laboulbeniomycetes, Leotiomycetes, Malacostraca, Maxillopoda, Micrococcales, Mortierellomycetes, Mucoromycetes, Perkinsea, Rhabditophora, Rhabdophorina, Tremellomycetes, Trichomonadea, Kinetoplastea, Clitellata; in orders: Actiniaria, Amphipoda, Amphisphaeriales, Blastocladiales, Bodonida, Capnodiales, Cephalaspidea, Chytridiales, Dermocystida, Ellobiophryidae, Entomophthorales, Eubodonida, Eucoccidiida, Eurotiales, Fecampiida, Haplosporida, Hymenoptera, Kentrogonida, Laboulbeniales, Mallophaga, Meiodihaplophasida, Micrococcaceae, Mortierellales, Mucorales, Multivalvulida, Neotaenioglossa, Nippotaeniidea, Paramyxida, Perkinsida, Peronosporales, Pleurostomatida, Poecilostomatoida, Polyopisthocotylea, Rhynchobdellida, Sordariales, Tremellales, Trichosphaeriales, Tylenchida, Xylariales, Trichomonadida. Moreover, a few pathogen species not classified to phylum, class or order (5 prions, 4 viruses and a single bacteria; Table S2) were excluded from the analyses.

Infestation of different families/classes of the studied plant/animal hosts was analysed with the number of recorded pathogens counted per host as a response variable. One model was created for plant and one for animal hosts. The two models included the following fixed effects: the host taxonomic group (family/class), the number of scientific papers on host infestation, its native range and environment, and type of introduction. Interactions between family/class and other variables (‘family/class * native range’, ‘family/class * habitat’, ‘family/class * type of introduction’) were also included. Each of the two base models, for plants and animals, was used to generate best-fit models with the lowest corrected Akaike information (AICc) and delta (Δ) values (Table S3). In order to indicate strong evidence for the model, the criterion with $\Delta < 2$ was taken into consideration (Burnham and Anderson, 2002). Best-fit models were selected using the ’dredge’ function from the ‘MuMIn’ package (Bartoń, 2016). Importantly, only a single interaction was statistically significant among the all best-fit models, namely, the interaction between class and native range of animal hosts (Table S3). To test the differences obtained with the interaction, the data was reduced to the respective host class and then the best-fit model without ‘Class’ variable and ‘Class * Native range’ interaction was created.

We conducted also another set of analyses of host infestation, analogical to the ones described above. We used the same variables and interactions, however, the essential exception was that only viruses and bacteria were taken into account (Table S3).

3. Results

The level of knowledge on the alien species acting as parasite hosts was very variable: for 13 species no scientific papers was found whatsoever, whereas as many as 806 papers were available for *Crassostrea gigas* (Table 1; Tables S1 and S2). On average, there were about 40 papers associated with pathogens per single host ($\overline{x} = 38.9$, S.D. = 94.13). Moreover, information on pathogen-host associations was very dispersed, with significant discrepancies between the explored data sources: for as many as 1316 records (267 in plant and 1049 in animal hosts), information on a specific pathogen-host association was found only in a single data repository; only 125 associations (18 in plants and 107 in animals) were reported in 2 sources, and 11 (1 in plants and 10 in animals) associations – in 3 sources. The maximum number of data sources consistently reporting on specific pathogen was 4 but this was the case only in 5 animal hosts.

The total number of records on pathogens carried by the assessed species was 2096 (Table S4), with 452 records for the plant hosts (21.6%) and 1644 records for the animal hosts (78.4%). Records with pathogens identified to the level of genus accounted for 14.9% of all records (N = 313; Table S4) and the highest number of such unidentified species was among Platyhelminthes, Nematoda and Proteobacteria. Collectively, these 3 phyla accounted for more than a half of the total records at the level of genus. However, considering the share of records, only Proteobacteria, with 26.0% of reported records (Table S4) represent a phylum for which pathogens were commonly identified only to the level of genus. Similarly, there were Spirochaetae (37.0%; Table S4) and Chlamydiae (45.5%; excluding those with the total number of records lower than 10; Table S4). It needs to be stressed, however, that because for a single host, records of the same unspecified genus were only counted once, irrespective of the real number of occurrences (see Methods), the actual incidence of cases in which pathogen species were not precisely identified, was certainly higher.

There were 10 host species (8.47% of the species assessed) for which no information on pathogens was found in the explored data sources. Notably, all of them were plants (see hosts with ‘No data’ in the number of pathogen species in Online sources in Table 1). In addition, for one plant host *Gunnera tinctoria* it was not possible to identify any of its pathogens to the level of species; yet this species had two pathogen records at the genus level (Table S1). The remaining 106 hosts (48 plants and 58 animals) carried a total of 1303 different pathogen species (Tables S1 and S2), including 312 pathogens of plants, 994 pathogens of animals, and 3 pathogens (*Alternaria alternata*, *Ceratocystis fagacearum* and *Vibrio cholera*), recorded both in plant and animal hosts. Over threefold difference in parasite load between the analysed plants and animals was kept when the number of host-pathogen associations is considered, with 405 and 1377 associations, respectively. The recorded pathogens belonged to 48 different phyla (plant hosts: 17, animal hosts: 44), 89 classes (plant hosts: 33, animal hosts: 76) and 188 orders (including species identified to genus; plant hosts: 64, animal hosts: 151; Tables S1 and S2). Pathogen diversity at each of those 3 taxonomic levels was 2.3 to 2.6 times lower among plant hosts than among animal hosts: plants hosted 17 different phyla, 33 classes and 64 orders of pathogens, while the respective numbers for animals were 44, 76 and 151. A total of 14 phyla, 20 classes and 27 orders of pathogens were recorded both in plants and animal hosts (Tables S1 and S2).

3.1. The dominant pathogens

The most widespread pathogen species infesting plants was bacteria *Xylella fastidiosa*, found on 7 host species (Table S5). The most widespread pathogen species in animals was Rabies virus, with 11 infested hosts (Table S5). It is noteworthy, however, that both in plants and in animals most pathogens occurred only in a single host: in plants it was the case for as many as 255 (81.7%) and in animals – for 778 (78.3%) of the recorded pathogen species (Table S6). The average number of hosts infested by a given pathogen was almost equal in plants ($\bar{x} = 1.3$; S.D. = 0.80) and in animals ($\bar{x} = 1.4$; S.D. = 0.99).

In plant hosts, we found significant differences between the number of occurrences of pathogen species belonging to specific phyla ($\chi2 = 52.40$, df = 11, $p < 0.001$; Fig. 1). Representatives of Arthropoda, with 105 recorded occurrences, were pathogens most frequently transmitted by plant hosts (Fig. 1). This taxon differed from all other phyla (at $p < 0.05$; Fig. 1), except for Tracheophyta; however, since in comparison with Tracheophyta the result was nearly significant ($p = 0.062$; Fig. 1), the dominance of Arthropoda was noticeable also in this case. The second important phylum was Ascomycota, with 99 recorded occurrences (Fig. 1); Ascomycota differed statistically from 6 of 11 remaining phyla (Basidiomycota, Kitrinoviricota, Nematoda, Oomycota, Proteobacteria and Tenericutes; at $p < 0.01$; Fig. 1). The numbers of occurrences of the remaining phyla did not differ between each other in most of cases (Fig. 1). Arthropoda and Ascomycota were also the most unique species-rich phyla. With 83 identified species each, they collectively accounted for more than a half of all recorded pathogen species (Fig. 1).

In plant hosts, differences between the recorded pathogen species were found also at the class level ($\chi2 = 46.96$, df = 20, $p < 0.0001$); Insecta was a group with the highest numbers of pathogens (both for the number of occurrences and the number of species; 97 and 75 respectively; Fig. 2) and differed statistically from 15 of 20 remaining classes (at $p < 0.05$; Fig. 2). In comparison between Insecta and Ustilaginomycetes, the result was nearly significant ($p = 0.056$; Fig. 2). In four comparisons of Insecta (and Magnoliopsida, Repensiviricetes, Sordariomycetes, Taphrinomycetes) – the results were non-significant ($0.75 < p < 0.98$). However, the number of hosts transmitting them was higher than the numbers of hosts in Magnoliopsida, Repensiviricetes and Taphrinomycetes (Table S1). Only Sordariomycetes, with over 20 records of both occurrence and unique species (Fig. 2), appeared to be significant in comparison with Insecta. The two other unique species-rich classes are also noteworthy – Dothideomycetes and Leotiomycetes. The sum of unique pathogen species recorded from those two groups was 31 and 25, respectively (Fig. 2); thus, only Insecta with 75 species, were more numerous.

Pathogen dominance in plant hosts was also tested using the order level, however, we found no statistical differences at this taxonomic resolution ($\chi2 = 15.18$, df = 36, $p = 0.9$; Fig. S1). Nevertheless, Hemiptera was the most unique species-rich group (Fig. S1). Although there no occurred many hemipteran pathogens within a single plant host, they were widely distributed across the hosts species (over 1/3 of them were infested by Hemiptera; Fig. S1).

Among the animal hosts, the differences between particular pathogen phyla were clearly significant ($\chi2 = 654.68$, df = 32, $p < 0.001$; Fig. 3). The dominant pathogen group was Platyhelminthes, with 309 occurrences of 242 unique species (Fig. 3). Prevalence of the Platyhelminthes significantly differed from all remaining phyla (at $p < 0.01$). We also noted a high number of pathogen species representing Nematoda, Arthropoda, Ciliophora and Ascomycota (Fig. 3). Those four phyla significantly differed from all the others (at $p < 0.05$), with the exception of Heterokontophyta and Zygomycota.

Differences between the recorded pathogens of animals were found also at the class level ($\chi2 = 602.04$, df = 50, $p < 0.001$; Fig. 4). The dominant class was Trematoda, differing from all remaining classes (at $p < 0.01$), and represented by the highest numbers of occurrences and unique species (Fig. 4). The next two important classes were Ciliatea and Chromadorea (Fig. 4); they were not different only from Insecta, Oomycota and Sordariomycetes. At the same time, it should be stressed that the importance of Chromadorea was probably higher than that of Ciliatea, because the former class was more widespread among the hosts than the latter one (Fig. 4). The following groups were also well-represented: Insecta, Arachnida, Oomycota and Sordariomycetes. Insecta did not differ only from 8 out of 51 classes (at $p < 0.05$) and they occurred frequently and in high number of unique species (Fig. 4). Interestingly, there were more pathogen species among Insecta than among Ciliatea (Fig. 4). The results for Arachnida, Oomycota and Sordariomycetes were also relatively high. They did not differ from 13, 14

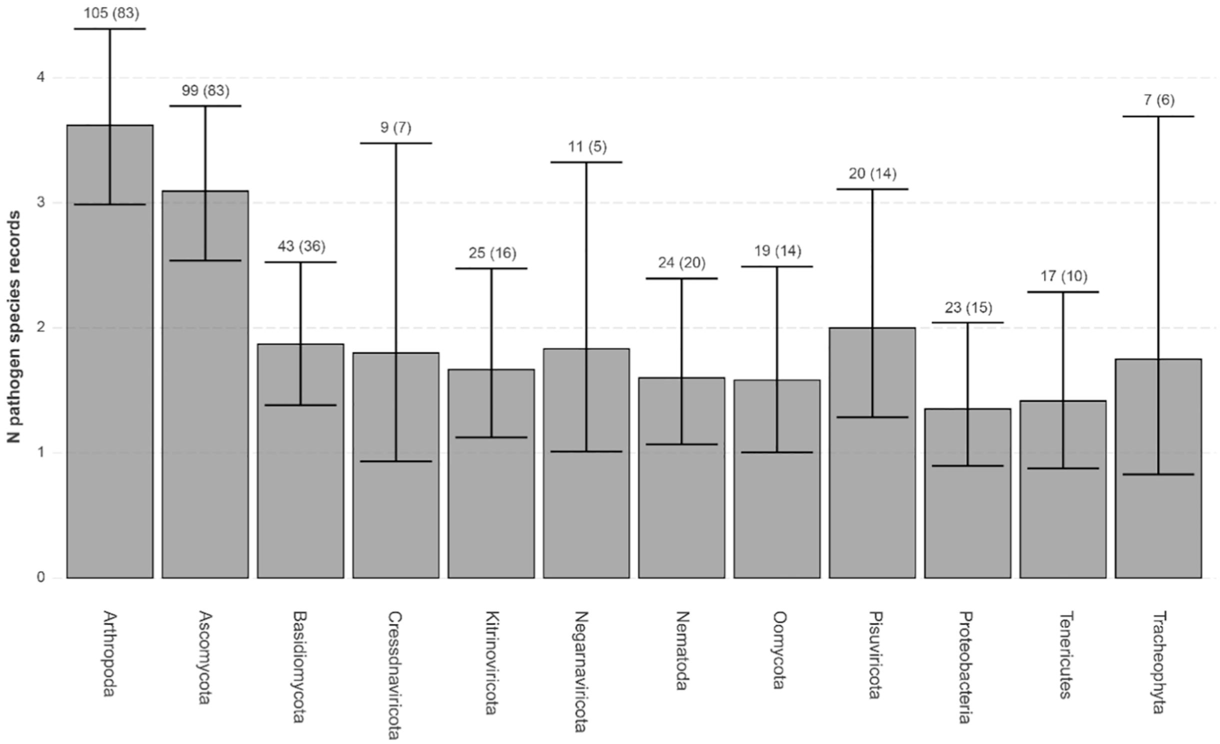

Fig. 1. The estimated number of records of pathogen species (±confidence intervals) in phyla transmitted by plant hosts. Numbers above the error bars and outside brackets indicate the number of occurrences of pathogen species from a given phylum, while the numbers in brackets indicate the number of unique pathogen species; the first value was used in the statistical model (see Methods).

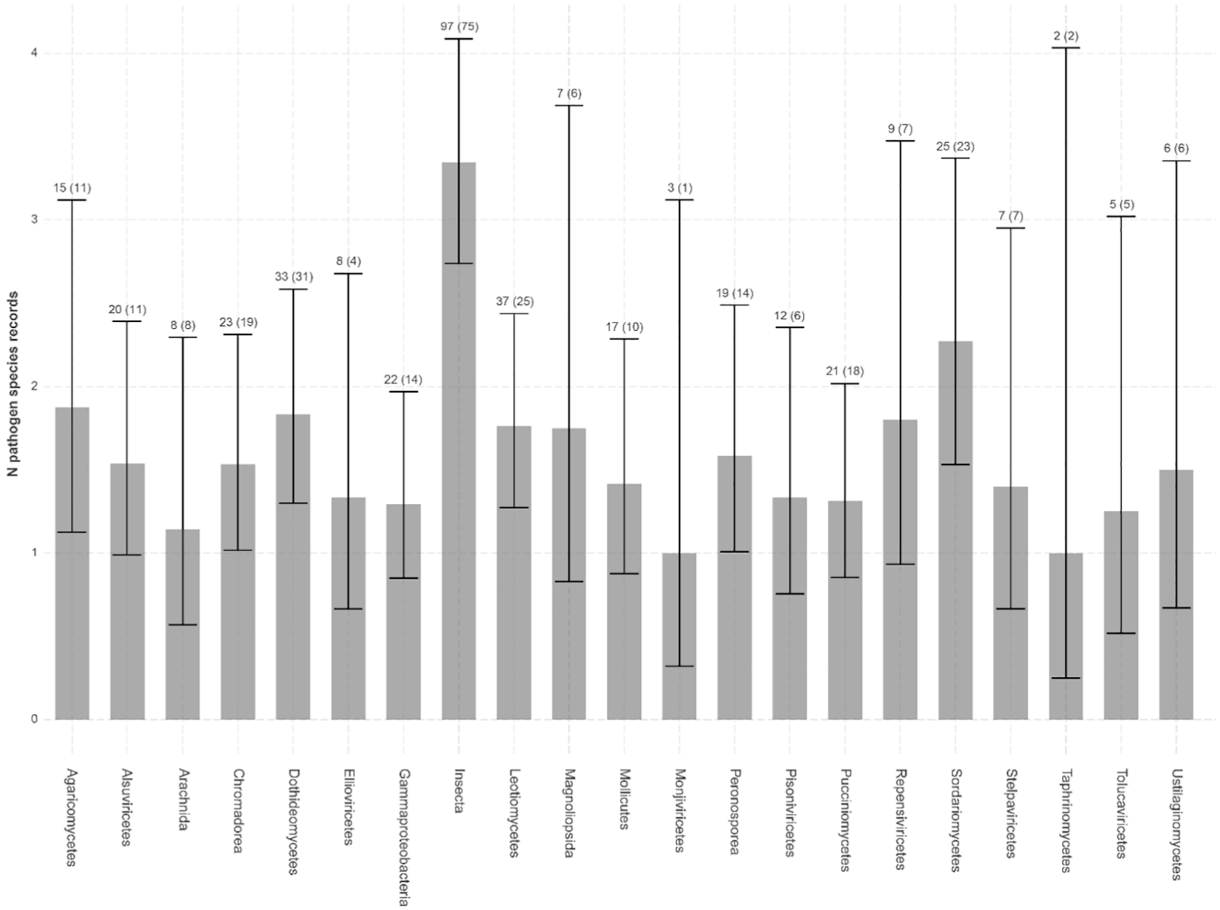

Fig. 2. The estimated number of records of pathogen species (±confidence intervals) in classes transmitted by plant hosts. Numbers above the error bars and outside brackets indicate the total number occurrences of pathogen species from a given class, while the numbers in brackets indicate the number of unique pathogen species; the first value was used in the statistical model (see Methods).

and 18 out of 51 classes, respectively (at $p < 0.05$); moreover, results of six comparisons for those classes were nearly significant ($p < 0.06$). Thus, the importance of those three classes should be noted. There were also two classes – Cestoda and Conoidasida – that occurred in many hosts, however, with low number of pathogen species (Fig. 4; Table S2).

The same analyses revealed differences also for orders of pathogen species recorded from animal hosts ($\chi2 = 365.09$, $df = 94$, $p < 0.001$; Fig. S2). Peritrichida had the highest estimated mean number of recorded pathogen species and did not differ only from 5 of out 95 other orders (Hypocreales, Plagiorchiida, Polymorphida, Strongylida, Saprolegniales). However, although the species of this order occurred frequently (Fig. S2), they infected a very low number of hosts (Table S2); this order was recorded solely from 5 fish species (Table S2). Thus, although Peritrichida could be very harmful for few hosts, its dominance among all animal pathogen orders is questionable. Similarly, Polymorphida and Hypocreales strongly infested their hosts (Fig. S2), however, the number of these hosts was low (3 and 2, respectively; Table S3). In turn, Plagiorchiida and Strongylida infested many host species (Table S2); these two groups occurred relatively frequently and in high number of unique species (Fig. S2). The two orders did not differ statistically from each other, however, they did differ from many other orders (Plagiorchiida – from 77 and Strongylida – from 79 orders, at $p < 0.05$). Therefore, we assume that Plagiorchiida and Strongylida should be considered as dominant orders among animal hosts. In addition, it should be also noted that Rhabditida, Eucoccidiorida, Ixodida and Strigeatida were widely distributed among hosts, with low estimated number of species per each host species (Fig. S2 and Table S2).

3.2. The most infested hosts – All pathogens

The native range of most host species covered North America and Asia (56 and 38 species, respectively) and most of them were terrestrial and freshwater (67 and 33 species, respectively). There were almost four times more species that were introduced intentionally, than those introduced unintentionally (92 and 26 species, respectively; Table 1).

The two most infested plant hosts were *Ambrosia artemisiifolia* and *Prunus serotina*, with 28 and 27 pathogens, respectively. *Robinia pseudoacacia*, *Quercus rubra* and *Rosa rugosa* had 23 pathogens each (Table S7). Except for *R. rugosa* the same plants remained in the top 5 after accounting for the number of publications available, joined by *Parthenium hysterophorus* (Table S7). Among the animal hosts, by far the most infested species was *Procyon lotor*, with as many as 133 pathogens. *Perccottus glenii* hosted 102, and *Neovison vison* – 80 pathogens (Table S7).

The differences in pathogen load between plant hosts belonging to various families were tested using the best fitted model with four significant fixed effects: the number of publications, native range, habitat and introduction type (Table S3). We found that the number of pathogen species carried by their plant hosts increased with the number of available publications on the host infestation ($\chi2 = 64.93$, $df = 1$, $p < 0.001$; Fig. S3). The native range of host was also a significant variable ($\chi2 = 47.61$, $df = 8$, $p < 0.001$; Fig. 5). Although 'Europe/Africa/Asia' was the native range category with the highest number of pathogens (Fig. 5), it was represented by one host species solely and, therefore, it should not be considered as the dominant one. In turn, North America was an origin area for 25 out of 48 hosts, and their pathogen load was

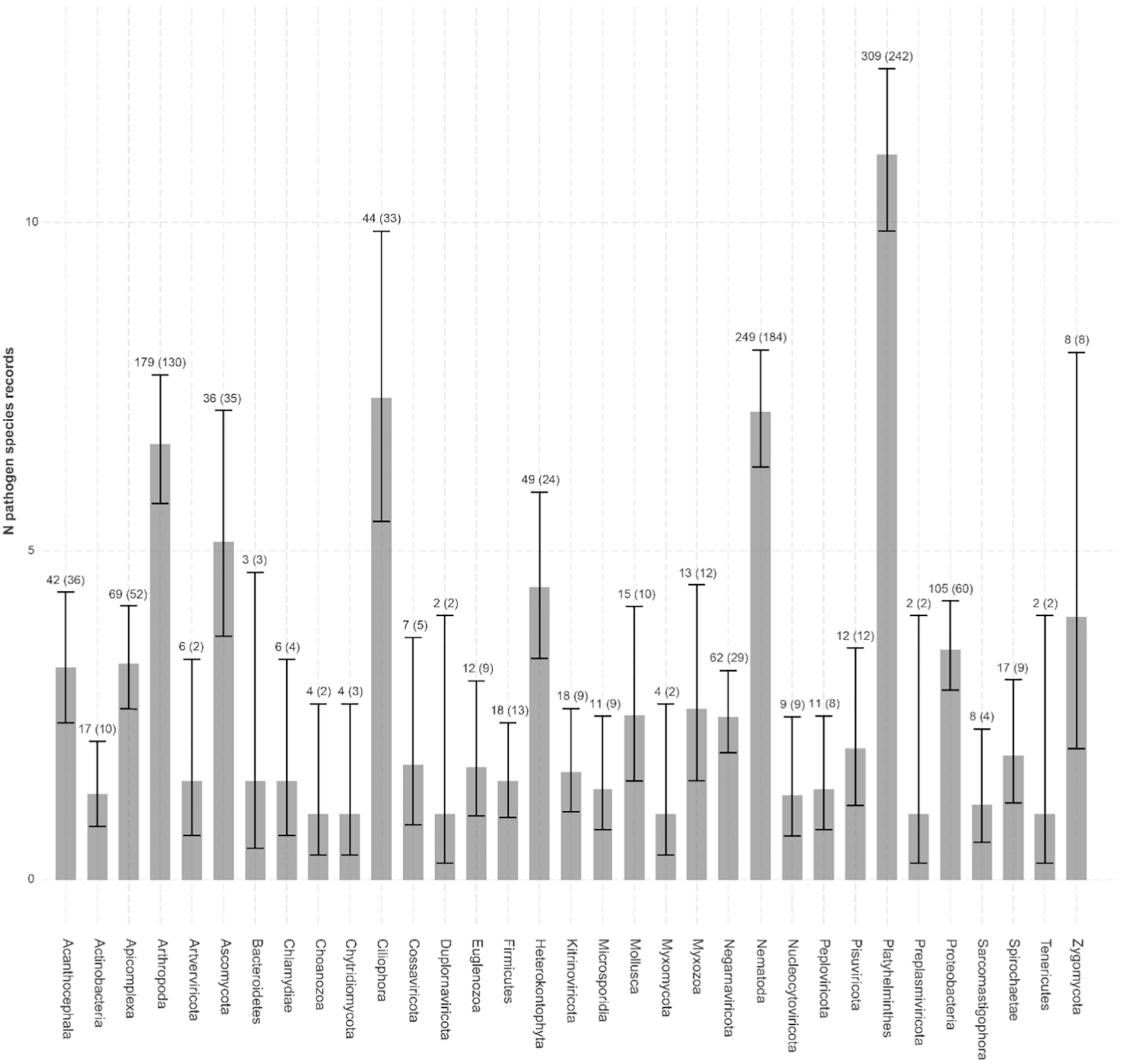

Fig. 3. The estimated number of records of pathogen species (±confidence intervals) in phyla transmitted by animal hosts. Numbers above the error bars and outside brackets indicate the total number occurrences of pathogen species from a given class, while the numbers in brackets indicate the number of unique pathogen species; the first value was used in the statistical model (see Methods).

statistically higher than in hosts from Africa/Asia, Europe, South America, and also for hosts with unclear origin (at $p < 0.05$ in all cases; Fig. 5). The only true competitor for the North American hosts were 12 Asian ones (Fig. 5); however, also in this case the dominance of the former group in terms of infestation level was noticeable (Estimate = -0.23, SE = 0.13, z = -1.76, p = 0.078). The differences were found also in the case of habitat and introduction type variables ($\chi2 = 4.84$, df = 1, p = 0.027; $\chi2 = 10.74$, df = 1, p = 0.001; respectively). In case of the former variable, significantly more pathogens were recorded from terrestrial hosts than from freshwater ones; in turn, considering the introduction type, results revealed that more pathogens were transmitted with unintentionally introduced hosts than with intentionally introduced ones.

Likewise in the plant hosts, the five variables (number of publications, class, native range, habitat, introduction type) and one interaction (class with native range) played a significant role in the analyses for animal hosts (Table S3). Also in this case the number of pathogen species carried by their hosts increased with the number of available publications on host infestation ($\chi2 = 162.02$, df = 1, $p < 0.001$; Fig. S4). We also found that host classes significantly differed in terms of pathogen load ($\chi2 = 258.43$, df = 7, $p < 0.001$; Fig. S5), with mammals as the most infested class. They differed from all other classes, except for Bivalvia and Insecta. It should, however, be stressed that while there were 20 mammalian hosts, Bivalvia and Insecta had only 4 and 2 hosts, respectively (Fig. S5). Moreover, the model revealed that the infestation level of hosts with North American native range was significantly higher than those from other regions (at $p < 0.05$; Fig. S6). At the same time, the result of the interaction demonstrated that the infestation level of classes differed between the particular native regions ($\chi2 = 110.30$, df = 5, $p < 0.001$; Fig. 6). For example, the mammalian hosts from North American were more infested than the Asian ones (contrast: Estimate = -0.66, SE = 0.11, z = -5.90, $p < 0.001$; Fig. 6), while the Asian hosts of Malacostraca carried significantly more pathogens than Malacostraca hosts from North America (contrast: Estimate = 0.79, SE = 0.41, z = 1.95, $p < 0.01$; Fig. 6). In turn, the avian hosts from four different regions did not differ statistically (in all cases $p > 0.1$; Fig. 6). We revealed differences also for fish hosts belonging to Teleostei; the Asian Teleostei hosts transmitted more pathogen species than those from North and South America (in both cases $p < 0.001$; Fig. 6). Americas also differed with respect to mammal hosts, with more pathogens from North American

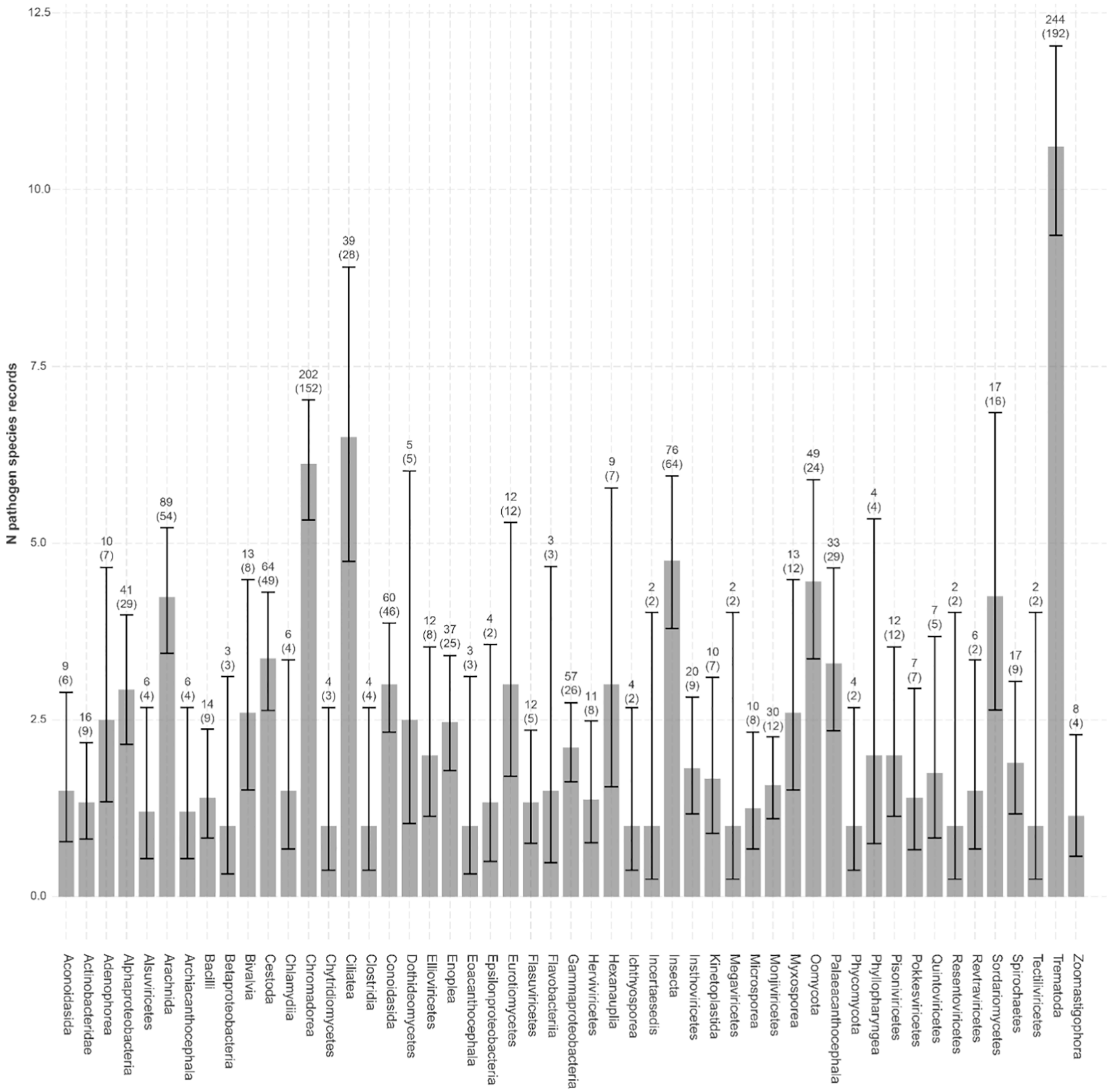

Fig. 4. The estimated number of records of the assessed pathogen species (±confidence intervals) in classes transmitted by animal hosts. Numbers above the error bars and outside brackets indicate the total sum occurrences of pathogen species from a given class, while the numbers in brackets indicate the number of unique pathogen species; the first value was used in the statistical model (see Methods).

ones (contrast: Estimate = -2.66, SE = 1.03, z = -2.57, p = 0.01; Fig. 6). It should be also noted that all alien hosts that belonged to Bivalvia and Insecta originated from Asia, while Gastropod hosts were all of European origin. In turn, the native range of all alien Reptilia and Tentaculata was in North America (Fig. 6).

As in the case of plants, habitat was also significant in the model for infestation of animal hosts ($\chi2 = 21.78$, df = 2, $p < 0.001$). Hosts from marine habitats carried significantly more pathogens than terrestrial and freshwater ones. Moreover, as in case of plants, unintentionally introduced animal hosts carried more pathogens than those introduced intentionally ($\chi2 = 10.72$, df = 1, p = 0.001).

3.3. *The most infected hosts – Viruses and bacteria*

If only viruses and bacteria are considered, the most infested plant host was *R. rugosa* with 15 recorded species, while the remaining hosts transmitted 11 (*A. artemisiifolia*) or less species (Table S7). Like in the previous analyses, we found that the number of viral and bacterial pathogens for a specific host increased with the number of publications on that host ($\chi2 = 4.52$, df = 1, p = 0.033; Fig. S7). However, none of the remaining variables or interactions played a significant role for the transmission of viruses and bacteria (Table S3). At the time it should be noted that Asteraceae and Rosaceae families accounted for more than a half (56.6%) of all viruses and bacteria species found in plants (33 and 27 species, respectively; Table S8); thus, their importance should be noted.

As a vector for viruses and bacteria, *P. lotor* remained the most infested animal host, with 46 transmitted species (Table S7), while other hosts transmitted 25 (*Oryctolagus cuniculus*) or less species. The positive relation between the number of publications and the number of viral and bacterial pathogens carried, held true also for animal vectors, including *P. lotor* ($\chi2 = 18.02$, df = 1, $p < 0.001$; Fig. S8). At the same time, the host class, introduction type or any of the interactions did not play any significant role (Table S3). In turn, the pathogen load differed depending on the host origin ($\chi2 = 39.97$, df = 6, $p < 0.001$; Fig. 7) and habitat type ($\chi2 = 66.22$, df = 3, $p < 0.001$). The single mammal host from South

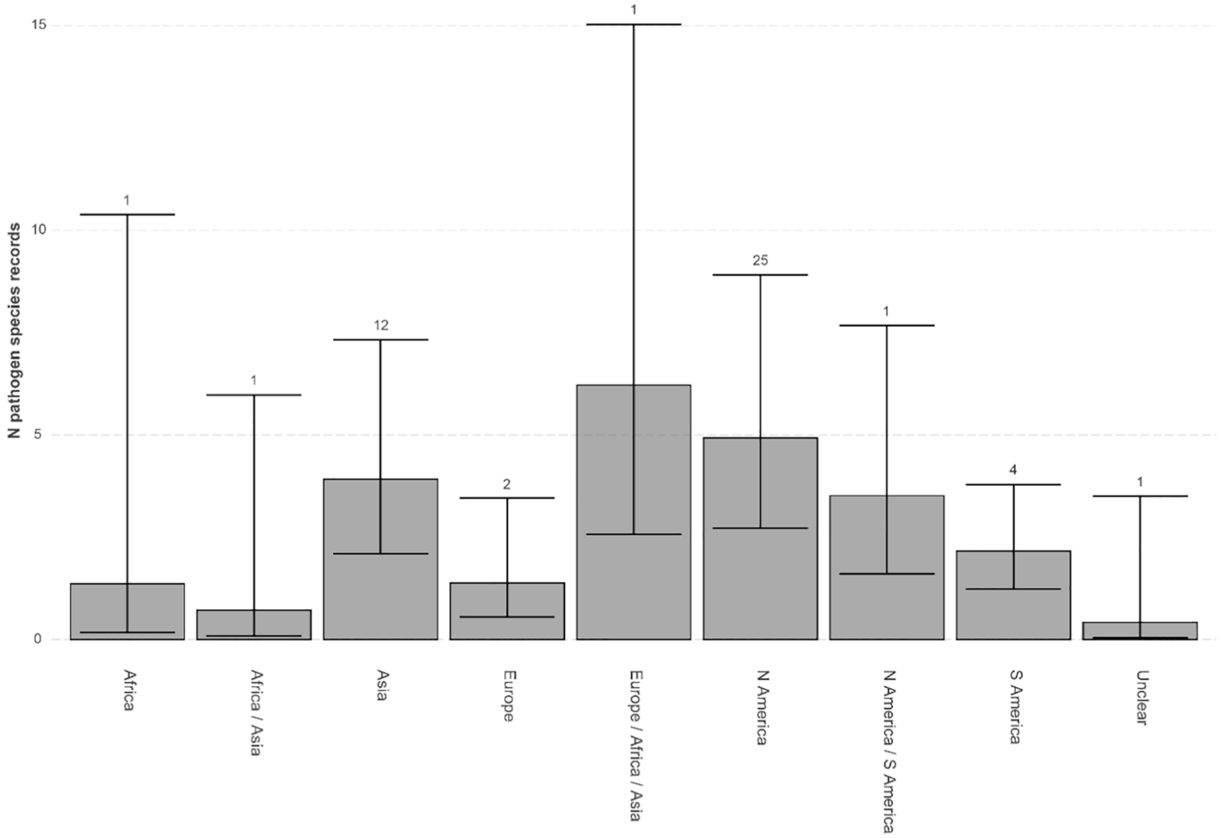

Fig. 5. The estimated number of pathogen species records transmitted by plant hosts from different native rages. Numbers above the error bars indicate the number of plant host species per native range.

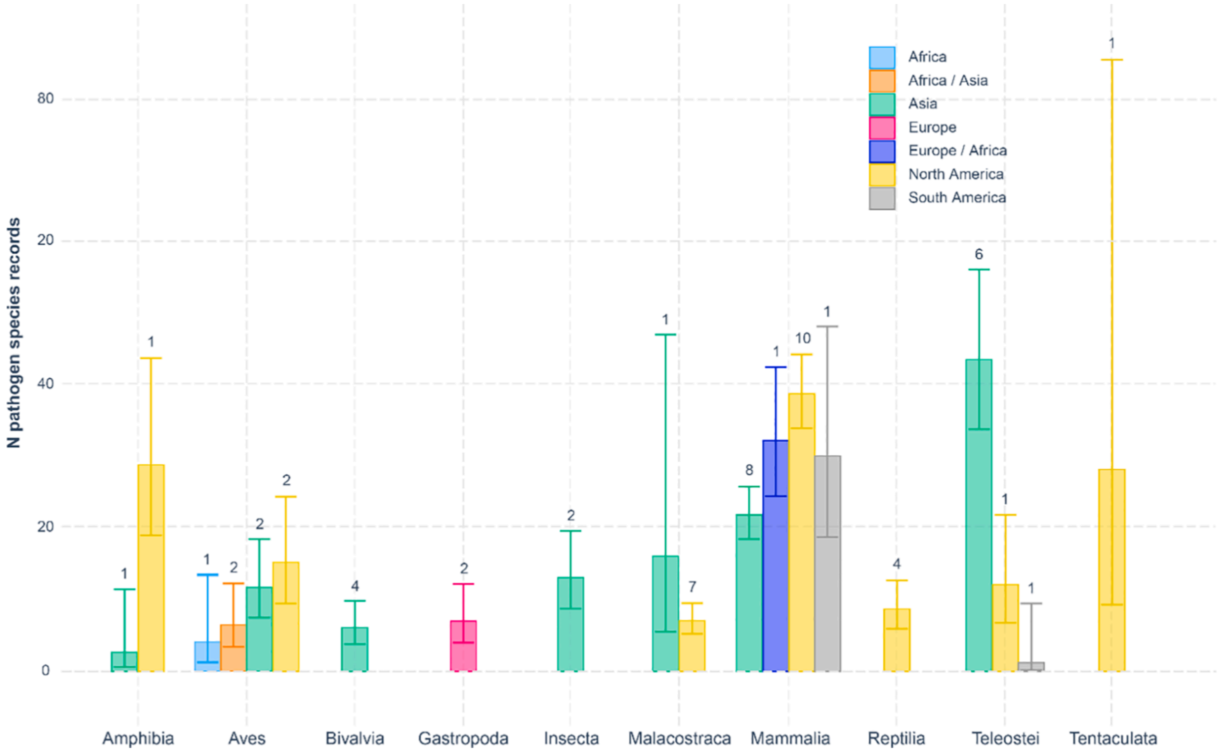

Fig. 6. The estimated number of pathogens transmitted by the animal hosts that differed in terms of class and native rage (±confidence intervals). Numbers above the error bars indicate the number of animal host species per native range.

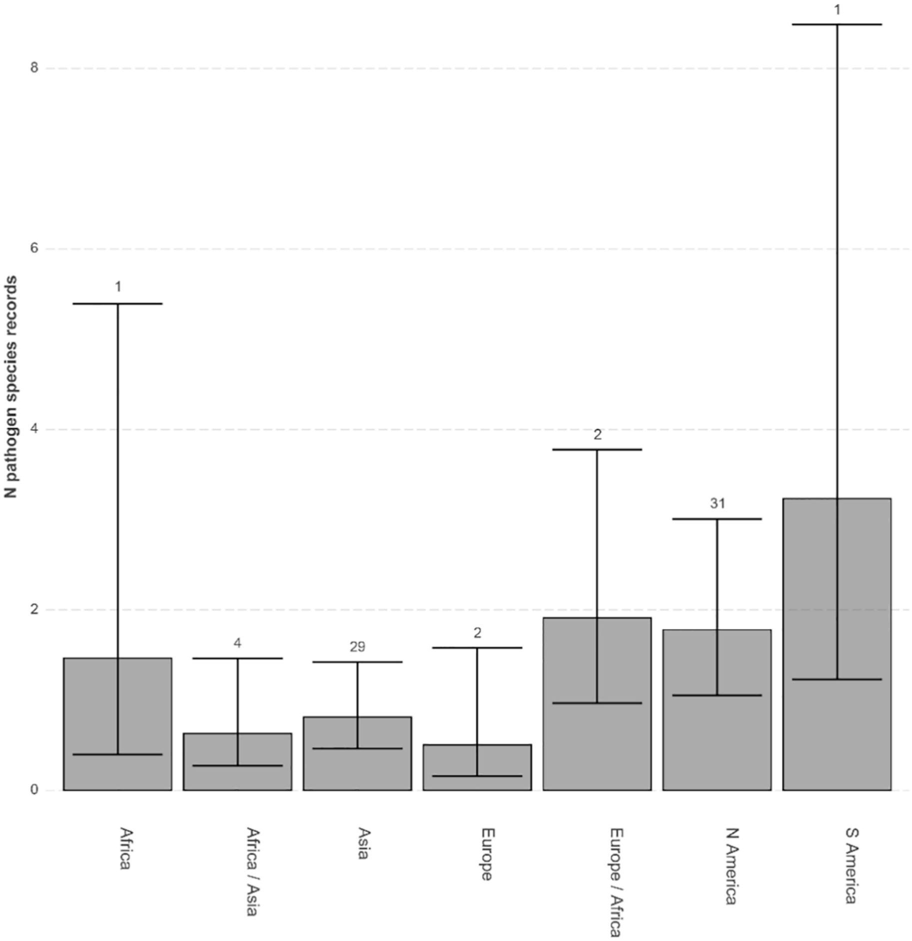

Fig. 7. The estimated number of viral and bacterial pathogen species transmitted by the animal hosts from different native rages. Numbers above the error bars indicate the number of animal host species per native range.

America, *Myocastor coypus*, transmitted most of all recorded species of viruses and bacteria (Fig. 7; Table S2). The result for this host significantly differed from those obtained for other hosts from Europe, and also from those from Asia and Africa/Asia (in all cases $p < 0.01$; Fig. 7). However, in comparison between the two most infested host native regions – North America and Asia (they included collectively 60 out of 70 host species; Fig. 7) – we found that the hosts from the former region are significantly more infected by viruses and bacteria than from the latter one (Estimate = -0.78, SE = 0.15, z = -5.34, $p < 0.001$; Fig. 7). Regarding the habitat, the terrestrial hosts (N = 39) transmitted more viral and bacterial pathogen species than the hosts from other habitats (in all cases $p < 0.001$). Although the 'Class' variable was non-significant in the model, it should also be noted that mammals transmitted 69.4% of all recorded viruses and bacteria (Table S8). It should at the same time be noted that mammals had the highest number of publications on their role as hosts (Table S8).

4. Discussion

Pathogens may be transmitted in many different ways, for instance, directly via air or water, or indirectly through infected food. Importantly, this flow is often driven by plant and animal hosts translocations that in turn may be associated with human activity (Wilkinson et al., 2011). Tens of millions of animals are transported outside of their native range every year. The plant and animal trade, both legal and illegal, brings multibillion-dollar financial benefits (Gippet and Bertelsmeier, 2021). As a consequence, pathogens are moved with their hosts all over the world, posing a serious threat for health of plants, animals and human in areas in which they arrive (Crowl et al., 2008; Dunn et al., 2012; Dunn and Hatcher, 2015; Kim et al., 2020; Swartz, 2002). A recent example of such pathogen pollution is the pan-global invasion of SARS-CoV-2 coronavirus, responsible for COVID-19 disease (Nuñez et al., 2020).

While it is acknowledged that the volume of the human-mediated movements of organisms is immense, the knowledge on associations between pathogenic microbes and their alien hosts, mechanisms of their introduction and impacts in new areas, remains very limited (Faillace et al., 2017; Roy et al., 2017; van der Putten et al., 2007). We demonstrated that only hosts important from a human perspective, including economically important (e.g., *C. gigas*, *M. coypus*) are well investigated in terms of their pathogens. However, even if case of best-studied species, the information on their pathogens is scattered among many sources, with few one-stop-shops. To partially bridge this gap, we collected a comprehensive dataset on pathogens, parasites and their vectors of 118 invasive alien plant species. Majority of these alien hosts are regulated under the European and/or Polish national legislature. We indicated both the most prevailing pathogen groups and the hosts that play a crucial role in their transmission.

4.1. *The dominant groups of pathogens*

The most widespread pathogens were bacteria *X. fastidiosa* in plant hosts, and Rabies virus in animal hosts. *X. fastidiosa* induces numerous plant diseases, including Pierce's disease, olive quick decline syndrome, citrus variegated chlorosis, almond leaf scorch and various other leaf scorch diseases. The historical occurrence of the species is associated with the Americas and also with Iran, whereas in Europe the species has been recorded since 2013 (EFSA et al., 2019). In turn, Rabies is a disease of almost all warm-blooded animals, including humans; it causes severe dysfunction of the central nervous system. In China, for example, rabies infections resulted in several hundred human deaths every year during 2015–2018 (Feng et al., 2020).

In case of plant hosts, Arthropoda was the dominant pathogen phylum, and Insecta was the dominant class – these groups were recorded in the highest numbers of host species. In turn, at the level of order only Hemiptera were relatively frequently recorded. It is noteworthy that these three dominant groups are strictly associated in terms of taxonomy. They include obligatory phytophages, parasites and pathogen carriers (Najberek et al., 2016). Notably, *A. fabae* was the most frequently recorded Hemipteran pathogen of plants. Its primary host is *Euonymus europaeus*, however, there are also over 350 secondary hosts of this aphid (Ellis, 2021; Wilkaniec, 2011). It feeds on sap of leaves of seedling and adult plants (wild and cultivated). It causes leaf deformation, decolorization and dieback. In addition, *A. fabae* itself is a host for over 30 virus species affecting plants (Ellis, 2021; Wilkaniec, 2011).

In case of animal hosts, the dominant phylum was Platyhelminthes, while Trematoda, that belong to Platyhelminthes, were the dominant class. However, as for plant hosts, it was difficult to indicate the dominant order. Only Plagiorchiida and Strongylida had relatively high number of species and they were carried by a wide range of hosts. The first order belongs to Trematoda and Platyhelminthes, and the most frequently recorded species was *Nicolla skrjabini*. This parasite has a lot of gammarid and fish hosts, while its first intermediate host is *Lithoglyphus naticoides* – an alien gastropod species in Europe (Mineeva, 2016). Among Strongylida, that belong to Chromadorea and Nematoda, the most frequently recorded species was *Ashworthius sidemi*. It is likely that the parasite was introduced in Europe with *Cervus nippon* and subsequently infested various ruminants, both domestic and wild (Demiaszkiewicz et al., 2018; Moskwa et al., 2015), including *Bison bonasus*. Importantly, *A. sidemi* may infect its hosts in a large numbers (greater than 40,000 specimens) and determine histopathological changes in the digestive system (Demiaszkiewicz et al., 2009).

4.2. The most infested hosts

We found that animals carried four times more pathogens than plant hosts, thus may pose a more serious threat in this respect. In our assessment, the most infested plant host was *A. artemisiifolia*, while in animals it was *P. lotor*. *A. artemisiifolia* is an annual herb native to Central and North America; nowadays, it is widely distributed across the world. The negative impact of *A. artemisiifolia* was widely demonstrated. For example, the species stimulates allergic diseases (rhinitis, fever and dermatitis) or incurs economic loses in crop cultivations (CABI, 2021a). The native region of raccoon is also in Central and North America. The species is considered as highly invasive in all areas in which it was introduced. Raccoons, for example, transmit the rabies virus; as we revealed, this virus was the most frequently recorded pathogen among all studied animal hosts (CABI, 2021b).

We did not find any differences in pathogen load between families of plant hosts, however, animal classes differed in this respect, with mammals as the most infected class. Interestingly, both in plants animals, hosts introduced from North America, namely *A. artemisiifolia* and *P. lotor*, carried the highest numbers of pathogen species. In animal classes we also found that the numbers of recorded pathogen species were associated with hosts' native region. For example, Asian Malacostraca or Teleostei carried more pathogens than their counterparts from North America.

The array of methods to reduce the risk of co-introducing alien pathogens is wider for intentional host introductions than for unintentional ones. For instance, intentionally introduced hosts may be subject to pre-import phytosanitary or veterinary controls (Hulme et al., 2008). Our analyses revealed that unintentionally introduced hosts, both plants and animals, carried more pathogens than those introduced intentionally. In this respect, a positive aspect is that almost four times more invasive alien hosts that we analysed were introduced intentionally. Interestingly, we also found that the level of infestation differs between broadly defined habitats. However, the results were opposite between plants and animals: terrestrial species were more infested in the former, while marine species – in the latter group. In alien plants most species (87.5%) were terrestrial, however, in animals there were only four marine hosts and each of them carried 10 pathogen species on average. Therefore, the result for animals is surprising. Nevertheless, it should be stressed that the first explanatory variable in the statistical model was the number of publications on pathogens, which accounts for the level of knowledge on the assessed host species. Thus, it is certain that this result was driven by very high number of articles (N = 806) available for Pacific giant oyster *C. gigas*.

Because of the paramount role of viruses and bacteria in epidemiology, we repeated analyses for those two groups separately. *R. rugosa* and *P. lotor* were the most infected hosts in this respect. We found also that in animals, viruses and bacteria were carried mainly by terrestrial hosts from North America. In case of plants we did not reveal any differences in this respect. Likewise, statistical models did not reveal domination in hosts occurring in particular habitats, or from particular taxonomic groups (families/classes). However, for the latter factor we found that Asteraceae and Rosaceae (in plants), as well as mammals (in animals), had significantly more viruses and bacteria, therefore should be considered as potentially posing more serious threat in their transmission. This result in plants may be partly due to the fact that they are well-investigated (see the number of publications per these groups), which is probably a consequence of the fact that in Poland they comprise high numbers if invasive alien species (Tokarska-Guzik et al., 2012).

It should be also noted that we identified several other pathogen-rich host species and taxonomic groups. It cannot be excluded that in more specific assessments (e.g., for avian viruses solely) their importance would increase.

4.3. Compiling the pathogen list as a challenging task

Compiling the information on pathogens of invasive alien species in Europe proved to be a very challenging task. The primary focus of the datasets we used was on alien species, and not on their pathogens as such. CABI was by far the most comprehensive source of information for the assessed species, while the amount of information available in the remaining data sources was fairly restricted. Consequently, there were few records on pathogen-host combinations that were consistently reported in more than a single data source. The paucity of information was only partially reduced after supplementing our efforts by extensive literature search. Another major difficulty was that the retrieved data was very heterogeneous in terms of taxonomic approach. Consequently, there were many inconsistencies in nomenclature and classification of the same taxa, not only between but even within the same data source. In addition, there was a considerable number of misspelled species names in the original data sources and some mistakes were replicated in more than one source of information. Discrepancies in taxonomy and mistakes in names were particularly apparent in microorganisms. Unification of the scattered and inconsistent information required a significant effort.

We found that in all analyses the number of recorded pathogens increased with the number of publications on the particular host as a vector. Our results may therefore reiterate that deficit of authoritative reference sources of information is one of the major problems in studying pathogens transmission in the context of biological invasions (Roy et al., 2017). Due to the dynamic character of the invasion process, updating IAS-oriented databases is challenging, even if resources are available. Moreover, there is a wide range of attributes of alien species presence that need to be addressed in the databases, including the cause, time and place of introduction, type of negative impact, or means to mitigate it. Consequently, collating and updating information on pathogens associated with alien species may not be a priority in database development.

On the other hand, some pathogen-oriented databases are available, such as Centers for Disease Control and Prevention (https://www.cdc.gov). While such focused data sources are more effectively updated in terms of host-pathogen interactions, they fail to provide a straightforward distinction between native and alien species, both with respect to hosts and their pathogens. From the perspective of studying and managing biological invasions, this is a significant drawback, as the native/aliens status of each species needs to be verified one by one. Unfortunately, it does not seem realistic to restructure the existing databases to accommodate biological invasion components what would make it easy to restrict the pool of species only to alien taxa. However, given the urgent need to provide a comprehensive and up-to-date information of pathogenicity of species moved across and between the continents, a practical intermediate solution would be forging direct links between the global databases on IAS, such as GRIIS (https://griis.org/), with databases dealing with pathogens.

This would, for instance, facilitate risk assessments of alien hosts by providing a one-stop-shop access to high-quality information on pathogens they carry. This is particularly important when one considers that a single risk-assessed alien host may carry numerous pathogens, often with debatable taxonomy. A risk-assessor, who usually is an expert in the host itself, rather than in its pathogen species, is therefore challenged with a task of collating and verifying information from distributed data sources, using different taxonomic systems. However, even the most efficient ways of distributing the existing data will not fill-in a major gap of very limited amount of information that is available for pathogens of some alien species, including even invasive ones (e.g., *I. parviflora, Sciurus niger* or *Neogobius gymnotrachelus*), let alone those whose invasive potential has not manifested yet.

CRediT authorship contribution statement

K. Najberek: Original research idea, Data collection, Data review and editing, Statistical analysis, Writing – original draft, Writing – review & editing. **A. Olszańska:** Data review and editing, Writing – review & editing. **B. Tokarska-Guzik:** Original research idea, Writing – review & editing, Funding acquisition. **K. Mazurska:** Writing – review & editing. **Z. Dajdok:** Writing – review & editing. **W. Solarz:** Original research idea, Data review and editing, Writing – original draft, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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