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ORIGINAL PAPER

The impact of invasive knotweed species (*Reynoutria* spp.) on the environment: review and research perspectives

Claude Lavoie

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Abstract I conducted an exhaustive literature review on Japanese knotweeds *s.l.* (including *Reynoutria japonica*, *R. sachalinensis* and *R.* ×*bohemica*), especially on the effects of these invasive plants on biodiversity and ecological processes or the chemical and physical characteristics of invaded habitats. A total of 44 studies have been published, the earliest in 2005, in peer-reviewed journals. Most studies were conducted in Europe, the others in the USA. Invasive knotweeds have major negative impacts on native plants, while the abundant litter produced and the deep rhizome system alter soil chemistry to the benefit of the invaders. However, the effects of knotweeds on other groups of species vary, with a combination of losers (soil bacteria, most arthropods and gastropods, some frogs and birds) and winners (most fungi, detritivorous arthropods, aquatic shredders, a few birds). This literature review highlights significant knowledge gaps of the effects of knotweeds on biodiversity (vertebrates) and ecological processes (ecohydrology). To what extent knotweed invasions have an impact on the population dynamics of native plants and animals on a regional to national scale remains to be verified. Although there is some evidence that knotweed invasions have negative effects on the environment, the research to date remains modest and a more extensive effort is needed to better define the environmental impacts of these plant invaders.

C. Lavoie (✉)
École supérieure d'aménagement du territoire et de développement régional Université Laval, Quebec City, QC G1V 0A6, Canada
e-mail: claude.lavoie@esad.ulaval.ca

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Introduction

Japanese knotweeds (*s.l.*), which include two species (Japanese knotweed: *Reynoutria japonica* Houttuyn [*Fallopia japonica* (Houttuyn) Ronse-Decraene]; giant knotweed: *R. sachalinensis* (F. Schmidt) Nakai [*F. sachalinensis* (F. Schmidt) Ronse-Decraene]) and their hybrid (Bohemian knotweed: *R.* ×*bohemica* Chrtek and Chrtková [*F.* ×*bohemica* (Chrtek and Chrtková) J.P. Bailey]), figure among the most invasive and problematic plant species of the world (Rumlerová et al. 2016). Japanese knotweed, the best known of the three taxa, was introduced from Japan to Europe in 1848 and to North America (New York State) about 1873 for horticultural purposes (Bailey and Conolly 2000; Barney 2006). The species escaped from gardens and is now widespread in its introduced range (Beerling et al. 1994; Barney 2006). Japanese, giant and Bohemian knotweeds spread rapidly once introduced, especially along riparian or road corridors where they form dense stands often extending over several hundred square meters (Pyšek and Prach 1993; Bímová et al. 2004; Tiébré et al. 2008; Rouifed et al. 2014; Duquette et al. 2016).

In 1999, the International Union for the Conservation of Nature (IUCN) selected Japanese knotweed as one of the 100 worst plant or animal invaders (Invasive Species Specialist Group 2016), following a selection process by experts that took into account the impacts on biodiversity and/or human activities, and the potential to illustrate important issues associated with biological invasions (Luque et al. 2014). Bohemian knotweed is also highly problematic from an environmental point of view. This hybrid is probably as, if not more widespread than Japanese knotweed in Europe and especially North America (Mandák et al. 2004; Bailey and Wisskirchen 2006; Gammon et al. 2007; Tiébré et al. 2007; Walls 2010; Gaskin et al. 2014; Duquette et al. 2016), and is more competitive than its parents (Parepa et al. 2014). Giant knotweed is less common than the two other knotweeds, but can locally form massive stands on riverbanks (Kappes et al. 2007; Topp et al. 2008; Skubała and Mierny 2009; Urgenson et al. 2009; Horáčková et al. 2014; Chmura et al. 2015).

There is a large body of literature on invasive knotweeds, especially regarding the biology, genetics and ecology of the taxa (see Barney et al. 2006 for the most recent review). Although knotweeds are largely perceived by environmental managers as a threat to biodiversity and the ecological integrity of ecosystems, and especially to riparian habitats (Pyšek et al. 2013; Cottet et al. 2015; Robinson et al. 2017), there is surprisingly no synthesis on the environmental impacts of knotweeds, apart that of Barney et al. (2006), written before the bulk of the literature on the subject had been published, and a very brief one (four papers reviewed) focusing only on soil properties (Koutika et al. 2011). To fill this gap, I conducted an exhaustive literature review on Japanese, giant and Bohemian knotweeds, especially on the effects of these plants on biodiversity and ecological processes or chemical and physical characteristics of invaded habitats. I also used this review to evaluate, with a scoring system, the effects of invasive knotweeds on the environment.

Methods

This literature review on invasive knotweeds, conducted with Web of Science™ (Reuters 2017) and Google Scholar (2017) search engines (last update: 22 March 2017), was restricted to studies published in peer-reviewed journals to avoid possible biases associated with other forms of communication. I did not presume non peer-reviewed reports were worthless, but I estimated an assessment of the impacts of knotweeds should first and foremost be based on studies that have been subjected to a formal evaluation process. In their *Handbook: scoring system for the impact of alien species* (updated version 6: Appendix S1 of Rumlerová et al. 2016), Nentwig et al. (2016) also suggested to preferably use information published in scientific journals for analyzing the impact of an invasive species. Keywords used with search engines were '*Fallopia*' OR '*Reynoutria*' OR '*Polygonum cuspidatum*' OR '*knotweed**'. Each work retrieved was screened for relevance. The author of this paper can read English, French, Italian and Spanish, but it is likely that some papers published, for instance, in German, were missed. The format of this review is similar to that used by Lavoie (2010) on the environmental impact of purple loosestrife (*Lythrum salicaria* L.): all effects, positive, negative or null, were noted and summarized in a table.

This literature review was also used as a tool to more precisely evaluate the impact of knotweed species on the environment with the Generic impact scoring system (GISS) proposed by Nentwig et al. (2016) and Rumlerová et al. (2016). The intensity of impact was quantified by a six level scale ranging from 0 (no impact detectable) to 5 (the highest impact possible). Six categories were used for assessing the environmental impact, i.e., effects on (1) plants or vegetation, (2) animals, (3) native species through competition, (4) native species through the transmission of diseases or parasites, (5) native species through hybridization, and (6) ecosystems. For a better comparison of results with previous studies that used GISS for assessing not only environmental but also socio-economic impacts, I completed the score with an analysis of the effects of knotweeds on human infrastructures, health and social life, the only socio-economic aspects on which invasive knotweeds potentially have an impact (Rumlerová et al. 2016). For this, I used the best information available from peer-reviewed literature, which was unfortunately scanty. Attributing a score to each category of impacts remains a subjective exercise, and I followed as closely as possible the instructions provided by the guide of Nentwig et al. (2016; Appendix S1 of Rumlerová et al. 2016).

Impact of knotweeds

A total of 44 studies were published, the earliest in 2005, in peer-reviewed journals on the effects of knotweeds on the environment (Table 1), especially on fungi, bacteria or amoebae (8), vascular plants (23), invertebrates (11), amphibians (1), birds (2) and ecological processes or chemical and physical characteristics of invaded habitats (21). Japanese knotweed was by far the most studied taxa (34 papers), followed by Bohemian knotweed (13) and giant knotweed (9). Most studies (31) were conducted in Europe (Belgium, Czech Republic, England, France, Germany, Ireland, Italy, Poland, Switzerland), while 13 were conducted in seven US states (Idaho, Massachusetts, New Jersey, New York, North Carolina, Pennsylvania, Washington). There were more correlative observational studies (field surveys: 30 papers) than manipulative experiments (16).

Fungi, bacteria and amoebae

Most studies detected a higher abundance, biomass and/or species richness of fungi and amoebae, and a lower bacterial abundance or biomass, in knotweed stands (mostly Japanese knotweed) than in non-invaded sites. The slowly decomposing knotweed litter probably favours fungi over bacteria, as a result of their greater ability to mineralize plant heteropolymers and their higher C-use efficiency (Mincheva et al. 2014; Tamura and Tharayil 2014; Stefanowicz et al. 2016). High concentrations of tannins in the litter of knotweed stands may also favour fungi over bacteria. Moreover, the decomposition of the polyphenolic compounds of knotweeds leaves requires enzymes that are essentially produced by a few fungal species (Suseela et al. 2016). However, two recent studies conducted in Poland showed that arbuscular mycorrhizal fungi are also negatively impacted by Japanese knotweed, probably because knotweeds are non-mycorrhizal plants (Stefanowicz et al. 2016; Zubek et al. 2016).

Vascular plants

All studies showed a negative effect of knotweeds on native plants for biomass, cover and/or species richness (up to 10 times fewer species in invaded areas), although some species are less impacted than others. The plant biomass in knotweed stands is much higher (up to 13 times) than that of adjacent non-invaded sites; this productivity and the high stem density contribute to the suppression of native forbs and herbs (Urgenson et al. 2009; Aguilera et al. 2010; Maurel et al. 2010; Chmura et al. 2015; Mincheva et al. 2016). Removing knotweed stands in riparian areas favours the restoration of native plant assemblages (Claeson and Bisson 2013; Urgenson et al. 2014). Some studies suggested that allelopathic compounds from knotweeds are at least partly responsible for growth reduction in native plants (Moravcová et al. 2011; Murrell et al. 2011; Dommanget et al. 2014). However, Parepa and Bossdorf (2016) recently showed that experimental results could be strongly influenced by the artificial potting substrates used for growing plants, and advocated for the use of natural soils in additional experiments before concluding on a real effect of knotweed compounds on the growth of native species.

Invertebrates

Various groups of species (beetles, mites, slugs, snails, springtails, etc.) have been studied to evaluate the effects of knotweeds on invertebrates. Knotweed invasions resulted in a mix of losers (e.g., mites, most riparian ground-dwelling beetles, snails, springtails) and winners (e.g., detritivorous species), while other groups of species (e.g., slugs) are apparently little impacted. The establishment of large knotweed stands can nevertheless significantly lower the biomass (up to 60%) of riparian macroinvertebrates. Dense stands reduce plant species richness and simplify the structural complexity of the habitat for invertebrates, which may contribute to lower diversity, especially for herbivores (Stoll et al. 2012). A lower availability of prey can in turn affect invertebrate predators like spiders (Gerber et al. 2008). Lower soil pH, the high acidity of the tough knotweed leaves, and a low availability of alternative herbaceous food resources could also be detrimental to herbivorous invertebrates (Kappes et al. 2007; Gerber et al. 2008). On the other hand, detritivorous species seem to benefit from the increased productivity and the resulting high-detritus supply in knotweed stands (Topp et al. 2008; Skubała and Mierny 2009). Large aquatic shredders with long life cycles may especially take advantage of slow-decomposing knotweed leaves, which remain

Table 1 Scientific studies on the environmental impacts (as stated by the authors themselves, i.e., positive: +, negative: −, null, not clearly stated:?) of Japanese knotweeds (JK *s.l.*, including *Reynoutria japonica* (RJ), *R. sachalinensis* (RS) and *R.* ×*bohemica* (RB)) invasions that have been published in peer-reviewed journals

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Fungi, bacteria and amoebae						
Aquatic hyphomycetes (various species)	RJ	England, France: field survey	n.a.	+	Higher species richness, biomass and spore production on RJ leaves than on those of *Quercus robur*	Lecerf et al. (2007)
Fungi (various species)	RB	Washington, USA: manipulative experiment	n.a.	?	Some differences for biomass on RB leaves compared to leaves from two other native species, but no clear patterns detected	Claeson et al. (2014)
Saprotrophic fungi (various species)	RJ	Italy: manipulative experiment	n.a.	+ or −	Higher (RJ leaf litter) or lower (RJ stem litter) total fungal loads compared to those of litter from native grassland plants	Mincheva et al. (2014)
Fungi and bacteria (various species)	RJ	Massachusetts, USA: field survey	n.a.	+ or −	About 3 times greater abundance of fungi in soils under RJ stands than in adjacent non-invaded sites, and 50% lower bacterial abundance	Tamura and Tharayil (2014)
Naked amoebae (various species)	RJ	New York, USA: field survey	n.a.	+	Higher density in soils under RJ stands than in adjacent non-invaded sites	Bischoff and Connington (2016)
Fungi and bacteria (various species)	RJ	Poland: field survey	n.a.	−	Lower soil respiration, urease and arylsulfatase activities, abundance of fungi and gram-negative bacteria, and fungal:bacterial ratio in soils of RJ stands than in those of adjacent non-invaded sites	Stefanowicz et al. (2016)
Fungi and bacteria (various species)	RJ	Massachusetts, New York, North Carolina, USA: field survey	n.a.	+ or −	Up to 8 times greater abundance of fungi in soils under RJ stands than in adjacent non-invaded sites, and 61% lower bacterial biomass	Suseela et al. (2016)
Arbuscular mycorrhizal fungi (various species)	RJ	Poland: field survey	n.a.	−	Lower levels of fungi colonization and abundance of dark septate endophytes in soils of RJ stands than in those of adjacent non-invaded sites	Zubek et al. (2016)

Table 1 continued

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Vascular plants						
Various species	RJ	New York, USA: field survey	20 m^2	–	Native species richness and cover lower in RJ stands than in non-invaded sites	Maerz et al. (2005)
Various species	RJ	Belgium: field survey	12 m^2	–	Aboveground biomass higher in RJ stands than in adjacent non-invaded sites	Vanderhoeven et al. (2005)
Various riparian species	RJ?, RS?, RB?	Poland: field survey	14,400 m^2	–	Species richness negatively influenced by JK cover during the course of the spring-summer-autumn seasons	Tokarska-Guzik et al. (2006)
Various species	RJ	Belgium: field survey	36 m^2	–	Species richness lower in RJ stands than in non-invaded sites. Up to 3–13 times higher biomass in RJ stands	Dassonville et al. (2007)
Various species	RJ	Belgium: field survey	36 m^2	–	About 5 times higher biomass in RJ stands than in non-invaded sites	Dassonville et al. (2008)
Various riparian species	RJ, RB	France, Germany, Switzerland: field survey	80 m^2	–	Lower species richness in RJ or RB stands than in grassland or bush-dominated sites	Gerber et al. (2008)
Various species	RJ, RS, RB	Czech Republic: field survey	480 m^2	–	Up to 86% lower species richness in RJ, RS and RB stands than in adjacent non-invaded sites	Hejda et al. (2009)
Various riparian species	RS	Washington, USA: field survey	780 m^2	–	Species richness and abundance (cover or density) of native herbs, shrubs, and juvenile trees negatively correlated with RS stem density	Urgenson et al. (2009)
Various species	RJ	Massachusetts, USA: field survey	66 m^2	–	Up to 2–10 times fewer species and 2–4 times higher biomass in RJ stands than in non-invaded sites	Aguilera et al. (2010)
Various species	RJ	Ireland: field survey	n.a.	–	Seed bank of RJ stands differs in species composition and relative abundance from that of non-invaded sites	Gioria and Osborne (2010)

Table 1 continued

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Various urban wasteland species	RJ	France: field survey	314 m^2	–	Species richness and total cover increases from the centre of RJ stands towards adjacent non-invaded sites	Maurel et al. (2010)
Calamagrostis epigeios, *Lepidium sativum*, *Urtica dioica*	RJ, RS, RB	Czech Republic: manipulative experiment	n.a.	–	Lower germination rate for seeds exposed to RJ, RS or RB leaf extracts	Moravcová et al. (2011)
Forbs (4 species) and grasses (2 species)	RB	Switzerland: manipulative experiment	n.a.	–	Up to 57% biomass loss for forbs exposed to RB competition	Murrell et al. (2011)
Forbs (7 species) and grasses (2 species)	RB	Switzerland: manipulative experiment	n.a.	– or Null	No negative effects on germination rate and early growth, but RB may cause life-history shifts for some species	Parepa et al. (2012)
Various riparian species	RJ	Switzerland: field survey	60 m^2	–	Lower species richness in RJ stands than in non-invaded sites	Stoll et al. (2012)
Various species	RB	Washington, USA: manipulative experiment	940 m^2	–	Predominantly native assemblages re-established in riparian sites after RB removal.	Claeson and Bisson (2013)
Lotus corniculatus, *Plantago lanceolata*, *Trifolium pratense*	RJ	England: manipulative experiment	n.a.	–	Higher biomass if grown in soils extracted from non-invaded sites than in those from RJ stands	Tanner and Gange (2013)
Populus nigra, *Salix atrocinerea*, *S. viminalis*	RJ	France: manipulative experiment	n.a.	– or Null	Lower aboveground and/or belowground biomass of *P. nigra* and *S. viminalis* exposed to leachates from RJ	Dommanget et al. (2014)
Various riparian species	RB	Washington, USA: manipulative experiment	125 m^2	–	Predominantly native assemblages re-established in riparian sites after RB removal	Urgenson et al. (2014)
Various species	RJ, RS, RB	Poland: field survey	360 m^2	–	Species richness and total cover negatively influenced by JK cover during the course of the spring-summer seasons	Chmura et al. (2015)

Table 1 continued

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Lolium perenne, *Trifolium repens*	RJ	Italy: manipulative experiment	n.a.	–	Height, aboveground biomass and specific leaf area reduced by RJ competition, but *T. repens* more impacted	Mincheva et al. (2016)
Forbs (5 species)	RB	Switzerland: manipulative experiment	n.a.	–	Dominance of RB over the other native forbs in a competition experiment, but strongly influenced by the potting substrate used for testing	Parepa and Bossdorf (2016)
Various riparian species	RJ	Poland: field survey	64 m^2	–	Lower species richness and native plant cover in RJ stands than in adjacent non-invaded sites	Stefanowicz et al. (2017)
Invertebrates						
Macroinvertebrates (various species)	RJ	Idaho, USA: manipulative experiment	n.a.	Null	No difference in the abundance found in mesh bags filled with RJ leaves compared to bags filled with leaves from two other native species	Braatne et al. (2007)
Gastropods (various riparian species)	RJ, RS	Germany: field survey	n.a.	– or +	Species richness and diversity, and density of individuals lower in RJ or RS stands than in *Urtica*-dominated sites. Higher abundance of detritivorous species in RJ or RS stands	Kappes et al. (2007)
Invertebrates (various benthic species)	RJ	England, France: field survey	n.a.	+	Higher occurrence of large shredders (Trichoptera) in a stream near RJ stands than near non-invaded sites	Lecerf et al. (2007)
Macroinvertebrates (various riparian species)	RJ, RB	France, Germany, Switzerland: field survey	n.a.	–	About 40% fewer individuals and 45–60% lower biomass in RJ or RB stands compared to sites dominated by native vegetation	Gerber et al. (2008)
Beetles (various riparian ground-dwelling species)	RJ, RS	Germany: field survey	n.a.	– or +	Species richness and abundance of individuals lower in RJ or RS stands than in *Urtica*-dominated sites. Higher abundance of detritivorous beetles in RJ or RS stands	Topp et al. (2008)

Table 1 continued

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Microarthropods (various mite and springtail forest species)	RS	Poland: field survey	n.a.	–	Species richness and abundance of individuals lower in RS stands than in non-invaded sites, especially for Acaridida and Oribatida, which may be affected by antifungal activity of phenolic compounds present in leaves	Skubała and Mierny (2009)
Invertebrates (various detritivorous species)	RJ	France: manipulative experiment	n.a.	+ or Null	Higher or similar abundance or diversity in RJ leaf litter compared to that made with leaves of native species	Bottollier-Curtet et al. (2011)
Gastropods (various riparian slug and snail species)	RJ	Switzerland: field survey	60 m^2	– or Null	Snail species richness and abundance lower in RJ stands than in non-invaded sites, especially for large or long-lived species. Low impact on slugs	Stoll et al. (2012)
Macroinvertebrates (various aquatic species)	RB	Washington, USA: manipulative experiment	n.a.	?	Different assemblages on RB leaves than on leaves from two other native species	Claeson et al. (2014)
Snails (various riparian species)	RJ, RS, RB	Czech Republic: field survey	3200 m^2	–	Species richness and abundance of individuals generally lower in JK stands than in non-invaded sites, but impact not consistent among the knotweed species	Horáčková et al. (2014)
Riparian snails (*Succinea putris*, *Urticicola umbrosus*)	RJ, RS, RB	Czech Republic: manipulative experiment	n.a.	– or Null	RJ and RB rejected as food sources, but not RS	Podroužková et al. (2015)
Amphibians						
Green frog: *Lithobates clamitans*	RJ	New York, USA: manipulative experiment	n.a.	–	No mass gain for frogs deposited in RJ stands during a period of 38 h	Maerz et al. (2005)
Birds						
Various riparian species	RJ?, RB?	Czech Republic: field survey	n.a.	–	Decreasing species richness with increasing proportion of JK cover	Hajzlerová and Reif (2014)

Table 1 continued

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Various riparian species	RJ	Pennsylvania, USA: field survey	n.a.	Null	No difference for species richness and overall abundance of individuals between levels of RJ cover	Serniak et al. (2017)
Ecological processes or chemical and physical characteristics of habitats						
Leaf decomposition rate	RJ	Idaho, USA: manipulative experiment	n.a.	Null	No difference compared to two other native species	Braatne et al. (2007)
Leaf decomposition rate	RB	Washington, USA: manipulative experiment	n.a.	Null	No difference compared to two other native species after 56 days	Claeson et al. (2014)
Litter chemistry	RS	Washington, USA: field survey	n.a.	–	Reduction (−70%) of the litter mass produced by native riparian species in RS stands compared to non-invaded sites. C/N ratio 38–58% higher for RS litter than for native woody species	Urgenson et al. (2009)
Litter chemistry	RJ	Massachusetts, USA: field survey	n.a.	–	Up to 23–85% higher lignin/N ratios in RJ leaf litter than in the litter of dominant native canopy species	Aguilera et al. (2010)
Litter chemistry and decomposition rate	RJ	Italy: manipulative experiment	n.a.	–	Slower (3–4 times) decomposition rate of RJ litter than that of a litter from native grassland plants, because of a lower N content and a higher C/N ratio in RJ leaves and stems	Mincheva et al. (2014)
Litter decomposition rate	RJ	England, France: manipulative experiment	n.a.	Null	No difference compared to native riparian shrubs or trees producing slow-decomposing leaf litter	Lecerf et al. (2007)
Nitrification or denitrification	RJ, RB	Belgium, France: field survey	n.a.	–	Lower ammonia and nitrite oxydizing bacteria enzyme activity and denitrification enzyme activity in RJ or RB stands than in non-invaded sites	Dassonville et al. (2011)

Table 1 continued

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Soil nutrients or chemical properties	RJ	Belgium: field survey	n.a.	?	Higher mineral nutrient concentrations in topsoils of RJ stands than in adjacent non-invaded sites, but no consistent patterns	Vanderhoeven et al. (2005)
Soil nutrients or chemical properties	RJ	Belgium: field survey	n.a.	–	Higher exchangeable nutrient concentrations in RJ stands than in non-invaded sites	Dassonville et al. (2007)
Soil nutrients or chemical properties	RJ, RS	Germany: field survey	n.a.	–	Lower pH and K content in RJ or RS stands than in *Urtica*-dominated sites	Kappes et al. (2007)
Soil nutrients or chemical properties	RJ	Belgium: field survey	n.a.	?	RJ can slow down soil organic matter dynamics by reducing C mineralisation, but no consistent patterns	Koutika et al. (2007)
Soil nutrients or chemical properties	RJ	Massachusetts, USA: field survey	n.a.	Null	No difference between RJ stands and adjacent sites for total N, total C, ammonification, nitrification and total N mineralization	Aguilera et al. (2010)
Soil nutrients or chemical properties	RJ, RB	Belgium, France: field survey	n.a.	–	Lower pH and moisture levels in RJ or RB stands than in non-invaded sites. C/N ratio higher in RJ or RB stands	Dassonville et al. (2011)
Soil nutrients or chemical properties	RJ	Switzerland: field survey	n.a.	Null	No difference between RJ stands and adjacent sites for pH, $CaCO_3$ and soil organic matter (%)	Stoll et al. (2012)
Soil nutrients or chemical properties	RJ	England: field survey	n.a.	Null	No difference between RJ stands and non-invaded sites for total N, PO_4^{3-} and K^+	Tanner and Gange (2013)

Table 1 continued

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Soil nutrients or chemical properties	RJ	Massachusetts, New York, USA: field survey	n.a.	–	In spring, 60% lower concentration of inorganic N and rates of N mineralization in the uppermost soil layers of RJ stands than in soils of adjacent non-invaded sites, but values as high or higher in RJ stands by fall. Similar seasonal trends detected for C and mineralizing soil microbial enzymes. Opposite seasonal pattern for concentrations of dissolved organic N and phenolic compounds: 3 times higher in RJ stands in spring, but similar values in fall	Tharayil et al. (2013)
Soil nutrients or chemical properties	RJ	Massachusetts, USA: field survey	n.a.	–	C content and the proportion of C resistant to oxidation 26% higher or 21% lower, respectively, in RJ stands than in adjacent non-invaded sites	Tamura and Tharayil (2014)
Soil nutrients or chemical properties	RJ	Massachusetts, New York, North Carolina, USA: field survey	n.a.	–	Two times higher concentration of flavonoids and monophenols in RJ stands than in adjacent non-invaded sites	Suseela et al. (2016)
Soil physical properties	RJ	France: field survey	314 m^2	–	Thickness of the A horizon decreasing from the centre of RJ stands towards adjacent non-invaded sites	Maurel et al. (2010)
Soil physical or chemical properties	RJ	Poland: field survey	64 m^2	– or Null	No significant differences for total and exchangeable metal contents, pH and organic matter content between RJ stands and adjacent non-invaded sites. Soils under RJ stands have lower (total P) or higher ($N–NO_3$) nutrient concentrations	Stefanowicz et al. (2017)

Table 1 continued

Organisms or characteristics impacted and studied	JK species (hybrid) studied	Study regions and methods	Total area invaded by JK and sampled to assess its impact[1]	Impact	Main conclusions	Reference
Water level	RJ	New Jersey, USA: field survey and manipulative experiment	n.a.	–	A patch of RJ (150 m^2) may lower the water level of an adjacent small stream.	Vanderklein et al. (2014)

[1] *n.a.* not available or not applicable

abundant in streams until they complete their entire development (Lecerf et al. 2007). Although knotweeds appear to be exclusively entomophilous in all naturalized ranges (Barney et al. 2006), their effects on pollinators and plant-pollinator networks have apparently not been studied to date.

Vertebrates

Only three studies have been conducted on the effects of knotweeds on vertebrates: one on the green frog [*Lithobates* (*Rana*) *clamitans* (Latreille, 1801)], the two others on riparian birds. Green frogs deposited in Japanese knotweed stands (n = 17) did not gain mass during a period of 38 h, probably because of low food availability, while 9 out of 16 frogs deposited in adjacent non-invaded sites gained mass (Maerz et al. 2005). The two studies on birds reached conflicting conclusions, but the no-impact study could be partly explained by a knotweed cover too low to have an observable effect on birds (Serniak et al. 2017). On the other hand, both studies showed that a few bird species (generalists) benefit from knotweed invasions, while the abundance of some others (invertebrate consumers) is negatively correlated with knotweed cover (Hajzlerová and Reif 2014; Serniak et al. 2017).

Ecological processes or chemical and physical habitat characteristics

The vast majority of studies on the effects of knotweeds on ecological processes and characteristics of invaded habitats examined litter decomposition or soil chemical properties. The abundant litter produced by knotweeds is different from that of most of the native plants they suppress, with a higher C/N or lignin/N ratio. Soils under knotweed stands have a thicker A horizon, lower pH, lower K and inorganic N (in spring) content, and higher mineral nutrient concentrations and C content than those of adjacent non-invaded sites, but at least seven studies did not find significant differences in litter decomposition rates or soil characteristics, which suggests that impacts depend on the native species knotweeds replace (Lecerf et al. 2007). Some authors estimate that a knotweed invasion prevents the re-establishment of native species through (1) a displacement of nutrients from deep soil layers to surface layers thanks to the deep root system of the plant (Dassonville et al.

2007), (2) N retention by a retranslocation of this nutrient from aboveground to belowground organs (Dassonville et al. 2011), or (3) a slower N cycling and a reduction of the accumulation of inorganic N in spring (Tharayil et al. 2013; Suseela et al. 2016). Only one study addressed the consequence of an invasion on local hydrology, and concluded that a patch of Japanese knotweed may remove sufficient water from the soil to lower the level of an adjacent small stream (Vanderklein et al. 2014).

GISS score

There was no evidence (Table 1) of differences in the environmental effects of Japanese and Bohemian knotweeds, so they were considered together for evaluating their impacts with GISS. Giant knotweed was not evaluated because of the low number of studies on this species. Table 2 provides detailed justifications on scores and references used. A total score of 18–19 was attributed to Japanese and Bohemian knotweeds for their combined environmental and socio-economic impacts.

Discussion

There is little doubt that invasive knotweeds have a negative impact on native plants (Fig. 1), and that the abundant litter produced and the deep rhizome system alter soil chemistry to the benefit of the invaders. The impact on soil is noteworthy, since disturbances of the nutrient cycling process by invasive plants have, to date, rarely been documented worldwide (Vilà et al. 2011). However, the effects of knotweeds on other groups of species vary, with a combination of losers (soil bacteria, most arthropods and gastropods, some frogs and birds) and winners (most fungi, detritivorous arthropods, aquatic shredders, a few birds), although overall, data suggest losers are probably more numerous than winners. It is thus reasonable to conclude that knotweeds are a threat to the biodiversity and ecological integrity of riparian ecosystems. The magnitude of this threat (or impact) can be classified as major, according to the classification system proposed by Blackburn et al. (2014), since knotweeds cause the local extinction of native species and lead to changes in the structure of communities and the abiotic or biotic composition of ecosystems. However, these changes are probably reversible –the system may recover its original state– since native plant restoration projects have been successfully conducted (Claeson and Bisson 2013; Urgenson et al. 2014).

The GISS scoring system provides a different perspective on the impacts of knotweeds. The total score of 18–19 was somewhat lower than that of Rumlerová et al. (2016; Appendix S3) for the same species, taking the maximum score in each category attributed to Japanese or Bohemian knotweeds (sum = 21). The main differences were for the score on the impacts of knotweeds on plants through allelopathy (1 vs. 3), which I considered minor because of lack of field evidence and potential experimental problems (Mincheva et al. 2016; Parepa and Bossdorf 2016), and on the impacts on human social life (2–3 vs. 4), because there is some evidence that an overemphasis of risks by environmental managers, control companies and media has inflated the societal perception of the risks posed by knotweeds (Cottet et al. 2015; Robinson et al. 2017). On the other hand, I gave higher scores for the impacts on animals and on plants through resource competition on the basis of the relatively abundant literature on these subjects. Regardless of the exact score, which remains subjective, Nentwig et al. (2016) estimated, on the basis of their experience evaluating 349 exotic species with GISS, that an invader with a score of 18–21 would be at the limit between medium and high impact species. The difference between this evaluation and that resulting from the system proposed by Blackburn et al. (2014) is related to a classification based on the highest level of deleterious impact associated with any of the impact categories, instead of a sum of scores for all categories (GISS).

This literature review highlighted significant knowledge gaps regarding the effects of knotweeds on biodiversity and ecological processes. Although there was a relatively good research effort on fungi, vascular plants and terrestrial (riparian) arthropods (Fig. 1), other groups of species, and especially vertebrates, have been virtually ignored. Studies have been conducted in several European and American regions, but most were local, so to what extent knotweed invasions have an impact on the populations dynamics of native plants and animals on a regional to national scale remains to be verified, as is the case for most plant invaders (Powell et al. 2013; Thomas and Palmer 2015a). Moreover, the total area investigated

Table 2 Scores attributed, using the Generic impact scoring system (GISS), to Japanese knotweed and Bohemian knotweed (considered together) for different categories of environmental and socio-economic impacts

Category	Score and justification	References used
Environmental impacts		
Category 1.1. Impacts on plants or vegetation through mechanisms other than competition	1 (minor impacts, only locally). Experimental studies, potentially influenced by the artificial potting substrates used for growing plants, suggested that allelopathic compounds from knotweeds are at least partly responsible for growth reduction in native plants, but the only field study testing this effect did not find evidence for an impact on grassland species	Moravcová et al. (2011), Murrell et al. (2011), Dommanget et al. (2014), Mincheva et al. (2016) and Parepa and Bossdorf (2016)
Category 1.2. Impacts on animals	3 (medium impacts, several species concerned). As a group, animals impacted by knotweeds are a combination of losers (most arthropods and gastropods, some frogs and birds) and winners (detritivorous arthropods, aquatic shredders, a few birds), although overall, data suggest losers are probably more numerous than winners	Maerz et al. (2005), Kappes et al. (2007), Lecerf et al. (2007), Gerber et al. (2008), Topp et al. (2008), Bottollier-Curtet et al. (2011), Stoll et al. (2012), Hajzlerová and Reif (2014), Horáčková et al. (2014), Podroužková et al. (2015) and Serniak et al. (2017)
Category 1.3. Impacts on species through resource competition	4 (major small scale impacts, decrease of species of concern). All studies on vascular plants showed a negative effect of knotweeds on native plants for biomass, cover and/or species richness. The productivity and the high stem density of knotweeds contribute to the suppression of native forbs and herbs (light and space competition)	Maerz et al. (2005), Vanderhoeven et al. (2005), Tokarska-Guzik et al. (2006), Dassonville et al. (2007, 2008), Gerber et al. (2008), Hejda et al. (2009), Aguilera et al. (2010), Maurel et al. (2010), Murrell et al. (2011), Stoll et al. (2012), Chmura et al. (2015), Mincheva et al. (2016) and Stefanowicz et al. (2017)
Category 1.4. Impacts through transmission of diseases or parasites to native species	0 (no impact known or detectable)	
Category 1.5. Impacts through hybridization	0 (no impact known or detectable)	
Category 1.6. Impacts on ecosystems	4 (major small scale effects, changes in soil properties). The abundant litter produced and the deep rhizome system alter soil chemistry to the benefit of the invader. However, significant knowledge gaps regarding the effects of knotweeds on ecohydrological processes exist, which prevents drawing definitive conclusions on impacts	Aguilera et al. (2010), Dassonville et al. (2007, 2011), Tharayil et al. (2013, 2014), Mincheva et al. (2014), Vanderklein et al. (2014), Suseela et al. (2016) and Stefanowicz et al. (2017)
Socio-economic impacts		
Category 2.4. Impacts on human infrastructure and administration	3 (medium impacts, high eradication costs, including pesticide applications). Although the effects of knotweeds on infrastructure has rarely been documented in peer-reviewed journals, substantial investments are made each year, especially in Europe, to eradicate the species	Barney et al. (2006), Alberternst and Böhmer (2011), Environmental Agency of the United Kingdom (2013) and Clements et al. (2016)
Category 2.5. Impacts on human health	1 (minor impacts, only locally). Pesticides, and especially glyphosate, are often used to control knotweeds, but most applications are essentially local	Hagen and Dunwiddie (2008), Bashtanova et al. (2009), Delbart et al. (2012) and Clements et al. (2016)

Table 2 continued

Category	Score and justification	References used
Category 2.6. Impacts on human social life	2 or 3 (minor to medium impacts). This plant is difficult to control in domestic gardens. It may cause accessibility problems to water bodies. These impacts are hard to precisely evaluate. Overemphasis of risks by environmental managers, control companies and media may result in unnecessary anxiety and expenditure by householders, and inflate societal perception of the risks posed by knotweeds	Cottet et al. (2015) and Robinson et al. (2017)
Total score	18–19	

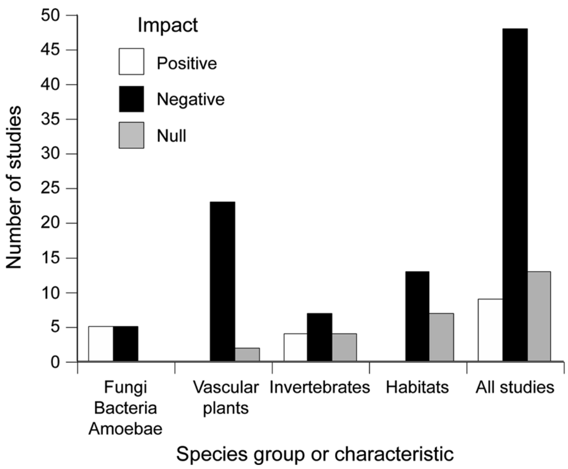

Fig. 1 Number of peer-reviewed studies reporting positive, negative or null environmental impacts of Japanese knotweeds (including *Reynoutria japonica*, *R. sachalinensis* and *R.* ×*bohemica*) for different groups of species or habitat characteristics. A study can have investigated several types of impacts, which explains why the total number of studies exceeds 44 (all studies)

for assessing the impact of knotweeds on plants was about 18 ha (Table 1), which represents a modest sampling effort: this includes the 14.4 ha study of Tokarska-Guzik et al. (2006). Fortunately, both field surveys and manipulative experiments on vascular plants point in the same direction (negative effects), which is not always the case for other plant invaders (Lavoie 2010).

One of the most striking results of this literature review is the near absence of ecohydrological studies (only one found: Vanderklein et al. 2014). Considering knotweeds essentially (albeit not exclusively) invade riparian habitats, hydrological processes or riverbank erosion should have attracted the attention of specialists, especially considering the presumed impact of knotweeds on the functioning of riparian ecosystems. For instance, Edwards and Howell (1989) mention (without supporting data) that in Wales, "*Japanese knotweed has displaced blocks used in urban flood protection schemes and its form could increase the risk of flooding in some river systems through the increase in frictional resistance to water flow*" (p. 222). The Michigan Department of Natural Resources (2012) writes "[Japanese knotweed] *can contribute both to stream bank erosion and flooding, when its large, fibrous stems wash into the water during periods of peak flow*" (p. 1). The Environmental Agency of the United Kingdom (2013) adds "*Japanese knotweed damages flood defence structure and reduces the capacity of channels to carry floodwater*" (p. 5). IUCN estimates knotweeds may "*increase the risk of flooding and river bank erosion as it establishes monospecific stand that die back in the winter leaving banks exposed*" (Invasive Species Specialist Group 2016). All are plausible hypotheses, but none have been rigorously tested, at least as indicated by publications in peer-reviewed scientific journals. More than 15 years ago, Tabacchi et al. (2000) and Tickner et al. (2001), and more recently Greene (2014), advocated for a more extensive research effort on the impact of riparian plant invasions on hydrogeomorphology. Knotweeds should figure on the top priority list for studies of this type.

Although there is some evidence that knotweed invasions have negative effects on the environment, the research effort to date (44 papers) remains modest. This is a common feature for invasive plants (Hulme et al. 2013): for instance, purple loosestrife, one of the five most intensively studied invasive species of the world (Pyšek et al. 2008), had been the object (in 2010) of only 34 studies for evaluating its impact on the biodiversity and functioning of wetlands (Lavoie 2010). The paucity of studies can feed skepticism about damages caused to biodiversity by plant invaders, which have recently been the subject of heated debates (see, for example, Simberloff 2013; Hulme et al. 2015; Thomas and Palmer 2015b). This skepticism can also be fueled by premature assertions that are not well supported by the scientific literature. For example, IUCN mentions in its account on Japanese knotweed (updated in 2010) that the species "*can reduce invertebrate biodiversity by half or more and reduce the quality of ecosystems for amphibians, reptiles, birds and mammals whose diets are largely composed of arthropods*" (Invasive Species Specialist Group 2016). The only study that can be used to support this assertion is that of Maerz et al. (2005), who treated a single species of frog, during a 38-h experiment with 17 individuals, which is not sufficient to extrapolate results to a large variety of amphibians, reptiles, birds and mammals. In conclusion, as urged by Hulme et al. (2013), "*it is (…) imperative that ecologists address these shortcomings* [i.e., ecological impacts are often assumed rather than proven] *to deliver a better quantitative evidence base for alien plant management*" (p. 212).

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

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