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The study of the spatial dynamics of Asian knotweeds (*Reynoutria* spp.) across scales and its contribution for management improvement

François-Marie Martin

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THÈSE

Pour obtenir le grade de

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Spécialité : **MBS – Modèles, méthodes et algorithmes en biologie, santé et environnement**

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préparée au sein du **Laboratoire IRSTEA – Laboratoire EcoSystèmes et Sociétés En Montagne**
dans l'**École Doctorale Ingénierie pour la santé, la Cognition et l'Environnement**

Apports de l'étude multiscalaire des dynamiques spatiales des renouées asiatiques (*Reynoutria spp.*) pour l'amélioration de la gestion

The study of the spatial dynamics of Asian knotweeds (*Reynoutria spp.*) across scales and its contribution for management improvement

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"I tell you, we are truly invaded by stuff coming from Asia" – A random guy

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– CHAPTER ONE: INTRODUCTION –



1. GENERAL INTRODUCTION

1.1. CONTEXT OF THE THESIS

1.1.1. Global change and biological invasions

The rise of mankind toward high technological advancements has only been possible at the cost of strong modifications of the various components of the *Earth system*. The profound changes at all scales¹ induced by anthropic activities have in many ways outcompeted natural processes. This has led some scientists to consider that the Holocene has in fact ended and that we have entered a new geological epoch called the *Anthropocene* (Crutzen, 2006). The Anthropocene is not officially recognized as a legitimate unit by geological authorities and one may, at first, find it pretentious to assume that our impacts are of comparable magnitude as that of telluric forces, meteor strikes or prolonged volcanic activities. Nevertheless, it is now evident that anthropic activities lead to modifications of Earth's surfaces and alterations of large scale climatic or biological processes that are so considerable that the impact of our development will probably still be observable in stratigraphic records for many millions of years into the future, thus justifying the use of a new term to refer to the current geological time (Zalasiewicz *et al.*, 2011; Lewis & Maslin, 2015).

In the Anthropocene, among the various and often highly graphic by-products of our socio-economic activities, such as deforestation, plastic islands in the sea, melting icecaps, or slaughtered baby-seals, most usually arouse the reprobation of the general public. On the other hand, there is a type of human-induced global change that presents the particularity of being quite ambivalent in the emotions it provokes to people; i.e. biological invasions (Vitousek *et al.*, 1996; Kueffer & Kull, 2017). Globalization and international trade has indeed led to a massive redistribution of species across the world (Westphal *et al.*, 2008), and some of the newly introduced species have become problematic for anthropic activities or nature conservation (Mack *et al.*, 2000; Vilà *et al.*, 2011). Some even argue that biological invasions are the second cause of species extinction behind habitat destruction and overexploitation (ISSG, 2008; Bellard *et al.*, 2016). If the introduction of species to new environments is not an unprecedented phenomenon and has occurred many times in history through *natural* or anthropic processes, the extent, magnitude, and potential for synergistic consequences of modern invasions is unique and should therefore be considered as a serious form of anthropogenic global change (Ricciardi, 2007; Kueffer, 2017).

Still, although very few people deny the importance of preserving biodiversity, questions related to exotic species and their management can often lead to passionate controversies between scientists, NGO's, decision makers and the general public (Selge *et al.*, 2011; Simberloff *et al.*, 2013; Courchamp *et al.*, 2017). Debates are particularly heated within the scientific community (e.g. Brown & Sax, 2004; Davis *et al.*, 2011; Richardson & Ricciardi, 2013), and the situation is becoming quite surrealistic as accusations of scientific *denialism* are starting to spread (Russell & Blackburn, 2017; Ricciardi & Ryan, 2018), to the dismay of many observers (e.g. Munro *et al.*, 2019).

¹ Throughout this thesis, we refer at the spatial extent of scales in the general sense (a large scale covers a large area), and not in the sense generally admitted by geographers (Wiens, 1989).

A possible reason for such conflicts is that our perception of introduced exotic species and their effects on *nature* is necessarily affected by our level of knowledge and experience on the subject, but also by our emotions (Young & Larson, 2011; Tassin & Kull, 2015). For the general public, this is easily reflected by the differences in the amount of sympathy granted to species (Courchamp *et al.*, 2017). If some potentially *harmful invaders* are invariably disliked by people (e.g. tiger mosquito, *Aedes albopictus*), others have many supporters (e.g. grey squirrel, *Sciurus carolinensis*). The level of empathy that people have for an animal species will have important consequences on their willingness to accept eradication campaigns (Fig. 1). Similarly, the aesthetic of an *invaded* landscape also influence the reluctance of people towards its management (Fig. 2; Vitousek *et al.*, 1996). For scientists, whom work ethic requires a high level of objectivity, it may not be so different (Larson, 2007). Conservation or invasion biologists are also emotional beings whose apprehension of *nature* and *invasions* are not devoid of subjectivity and cultural judgements (Larson, 2005; Tassin & Kull, 2015; Munro *et al.*, 2019). To a large extent, “the concept of biological invasions evokes a tension between what nature *is* and what nature *ought* to be” (Tassin & Kull, 2015), and even between biologists, different paradigms of nature may exist (Keulartz & van der Weele, 2009). Vehement and irrational conflicts possibly arise when these different visions collide.



Figure 1. Example of two invasive exotic species: *Badumna longinqua* (left panel), a lurking predator clearly born from your deepest nightmares, and *Felis sylvestris catus* (right panel), an adorable heart-melting predator. Although they both hunt down preys and lead to strong declines in biodiversity, they probably inspire very different feelings in most people.

Regardless of the way we consider nature, biological invasions are undeniably modifying the environment: e.g. decline of biodiversity, modification of biogeochemical cycles, changes in disturbance regime, biotic homogenization (Mack *et al.*, 2000; Ehrenfeld, 2010; Vilà *et al.*, 2011). The annual cost of biological invasions in terms of damages and management is estimated to be around \$120 billion in the United States (Pimentel *et al.*, 2005), and to exceed €12.5 billion in the European Union (Kettunen *et al.*, 2009). Although these estimations might be debatable, there are no doubts that biological invasions are costly. However, broad generalities on the impact of introduced exotic species are hard to establish, likely providing an additional explanation on the origin of the virulent disagreements between specialists (Davis *et al.*, 2011).



Figure 2. Invaded landscapes can sometimes be beautiful and may therefore have cultural values for some users. Here, a Californian roadside invaded by *Carpobrotus edulis* (Photo credit: www.plantright.org).

The difficulty to get a consensus on the actual magnitude of the impacts of biological invasions is, to a large extent, linked to the complex nature of these “invasions” and their manifestations in space and time. Firstly, not all introduced exotic species cause problems. Some introduced species are able to reproduce and maintain small populations in their new habitats but do not spread. Unlike *invasive* species, these *naturalized species* usually do not cause much large-scale damage (Richardson *et al.*, 2000; Kolar & Lodge, 2001). Conversely, the absence of apparent impacts or spread might sometimes only be related to time lags in the observations or in the effects (Crooks, 2005). Secondly, species (invasive or naturalized) can also have positive effects on ecosystems (MacDougall & Turkington, 2005) and their removal sometimes lead to unexpected and undesired negative impacts on natural systems (Zavaleta *et al.*, 2001; Bergstrom *et al.*, 2009). More generally, assessing the actual effects of any species is challenging. Invasive species can affect human health, economic activities, ecosystem functions and/or biodiversity either directly or through complex mechanisms and loops, that may furthermore change over time (Strayer *et al.*, 2006; Dostál *et al.*, 2013). A species may often induce simultaneously negative effects on one or several of these components while having positive effects on others (Vilà *et al.*, 2011; Tassin & Kull, 2015). When the picture is not all black and white and that, alongside invasions, ecosystems are modified by other forces, choosing to manage a particular invasive species indeed looks more like trying to maintain nature in a desired state that is conform to a certain vision rather than doing what is “good for nature”. Thirdly and finally, the impacts of biological invasions on biodiversity vary strongly depending on the scale of observation and the taxonomic groups considered. At local scale, a negative correlation is often found between native and exotic diversity, possibly as a testimony of the effect of the *biotic resistance* of communities (Naeem *et al.*, 2000; Shea & Chesson, 2002). On the other hand, higher spatial heterogeneity at larger spatial scale usually favours the coexistence of both types of species (Davies *et al.*, 2005), making predictions of

impacts at large spatial scales difficult to make (Theoharides & Dukes, 2007). Besides, if competition may lead to the local exclusion of species, it is very rarely associated with extinctions at the global scale (Gurevitch & Padilla, 2004; Sax *et al.*, 2007), hence the fact that extinctions induced by invasive plant species are almost never reported (Powell *et al.*, 2013). This represents a huge imbalance with invasive predators and pathogens that have been the cause of many species extinctions over time (Bellard *et al.*, 2016). Still, once again, lags may hide the long-term impacts of naturalized and invasive species (Tilman *et al.*, 1994; Strayer *et al.*, 2006), both positive or negative.

Because of the complexity of their impacts and underlying processes, biological invasions represent a fascinating field of studies that is highly multidisciplinary as they mobilise methods and notions from many disciplines such as biogeography, conservation biology, community ecology, landscape ecology or evolutionary biology. And despite some conflicts often related to the problems of the generalization of results, it seems that everybody acknowledges the high stakes related to invasions (Young & Larson, 2011). As a consequence, the need to better understand the dynamics of invasive species as well as their long-term effects and synergies with other components of global change fuels a prolific field of fundamental studies, while the necessity to prevent or address the consequences of invasions is increasingly accounted for by decision makers at all scales and offers many challenges for applied research.

1.1.2. Biological invasions: a process through space and time

Since Charles Elton and the early days of “invasion ecology”, our understanding of the way invasions occur has made considerable advances. Over the years, numerous hypotheses have been presented to explain invasions: e.g. enemy release hypothesis (ERH), biotic resistance, evolution of increased competitive ability (EICA), global competition, invasional meltdown, limiting similarity, novel weapons hypothesis (NWH), windows of opportunity, fluctuating resource, niche shifts (Catford *et al.*, 2009; Lockwood *et al.*, 2013; Jeschke, 2014). Furthermore, many conceptual frameworks and synthesis of invasion theory have been proposed (e.g. Davis *et al.*, 2000; Shea & Chesson, 2002; Mitchell *et al.*, 2006; Catford *et al.*, 2009; Blackburn *et al.*, 2011; Gurevitch *et al.*, 2011). Nonetheless, generalizations are still scarce and contradictory results have been found for many hypotheses (Moles *et al.*, 2012; Heger *et al.*, 2013).

The process of invasion, both symptom and cause of changes, may be viewed as a series of stages separated by various barriers that a species or a population has to cross in order to reach the next stage (Fig. 3; Blackburn *et al.*, 2011). And various factors may influence the success of a species/population at any given stage (Theoharides & Dukes, 2007). In this framework:

- An invasion begins with the transport of propagules from a species native range to a new region, therefore crossing a *geographic barrier*. If species can sometimes *naturally* cross the geographic barriers that form the borders of their native range, modern invasions usually start (voluntary or not) through anthropogenic transport vectors (Theoharides &

Dukes, 2007; Lockwood *et al.*, 2013). The probability of being transported is far from being equal between species or individuals. Some species are frequently transported because they possess *valuable* traits for anthropic activities (Mack & Lonsdale, 2001). Others are successfully transported because they possess traits that favour their survival during transport (Lockwood *et al.*, 2013).

- The second barrier, the *cultivation/captivity barrier*, is imposed by Humans in the case of voluntary introductions. It presents the particularity of being designed to favour the survival of the species/population (Blackburn *et al.*, 2011).

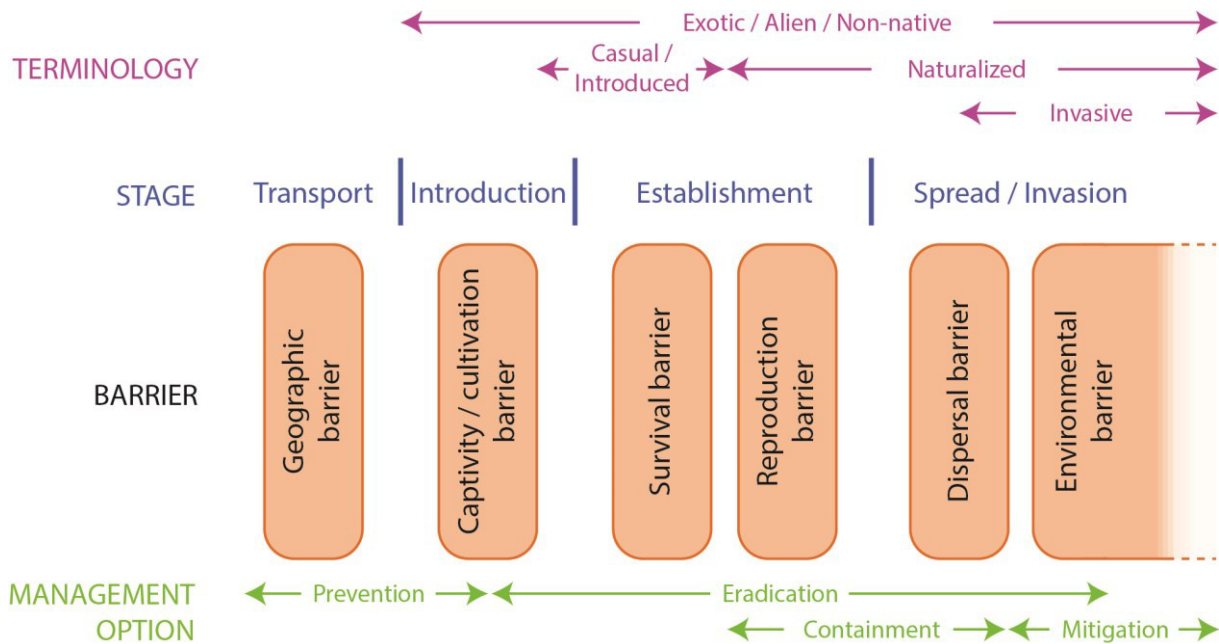


Figure 3. Conceptual representation of the invasion process. It can be viewed as a series of stages, in which barriers have to be overcome for a species/population to pass to the next stage. While progressing through the stages, a species/population will receive new denominations to better suit its nature. Relevant management options are also displayed (inspired by Blackburn *et al.*, 2011).

- After having been transported, or after having escaped cultivation/captivity, a species/population is introduced in a new ecosystem where it needs to *establish* and thus, cross *barriers of survival* and *reproduction* in order to produce self-sufficient populations. This stage may require several attempts and many years before it is successfully passed by a species (Richardson *et al.*, 2000; Blackburn *et al.*, 2011). *Survival* mainly depends on abiotic filters (e.g. climate, edaphic properties) and thus, on the characteristics of introduction sites. The survival probability of a species/population usually increases with increasing propagule pressure, genetic diversity, and phenotypic plasticity (Theoharides & Dukes, 2007; Richardson & Pyšek, 2012). Yet, to grow and establish, a population will have to overcome the biotic resistance (or biotic *containment*) of the recipient community (Levine *et al.*, 2004; Mitchell *et al.*, 2006). The outcome of the establishment stage therefore depends on the right combination of both the attributes of the introduced species (i.e. traits related to its *invasiveness*: e.g. speed and timing of growth, phenology, resource use efficiency, strong competitive abilities) and those of the colonized

community (i.e. related to its *invasibility*: e.g. functional diversity, resource availability, disturbance regime)(Richardson & Pyšek, 2006; Theoharides & Dukes, 2007; Wolkovich & Cleland, 2010; Gallien & Carboni, 2017). As both abiotic and biotic conditions are often changing, characteristics that promote persistence in the wait for more favourable conditions (e.g. clonality) may be particularly useful at this stage (Williamson & Fitter, 1996), and establishment success globally increases with residence time (Kolar & Lodge, 2001; Richardson & Pyšek, 2006).

- Finally, if a species/population manages to successfully and frequently reproduce, it may possibly cross a *dispersal barrier* that can truly make it an “invasive species” (Richardson *et al.*, 2000; Blackburn *et al.*, 2011). Quite frequently though, there is a lag phase between establishment and large scale spread (Pyšek & Hulme, 2005; Theoharides & Dukes, 2007), explaining why residence time is so strongly associated with invasion success (Richardson & Pyšek, 2006). The rate of spread and landscape expansion of a species mainly depends on its dispersal abilities and demographic properties as well as on landscape characteristics: e.g. heterogeneity, disturbance regime, number and distribution of dispersal corridors and suitable habitat patches (With, 2002; Hastings *et al.*, 2005; Theoharides & Dukes, 2007; Vilà & Ibáñez, 2011). As the invasive populations of a species spread and thus expand its range, the environmental conditions they encounter will increasingly differ from the conditions of the species introduction sites (Blackburn *et al.*, 2011). In the conceptual framework of Blackburn *et al.* (2011), this increasing variance in conditions is an *environmental barrier* that a species has to cross to become “fully invasive”. In Figure 3 however, this barrier is endless since there is probably no species that is able to grow in all possible existing conditions, meaning that even the most invasive species will eventually fail to spread and establish when it reaches the limits of its potential range (cf. Holt & Keitt, 2005; Alexander & Edwards, 2010).

Naturally, countless species and populations fail to become invasive because of any one of these barriers. Even highly invasive species sometimes end up declining, a phenomenon called *boom-bust dynamics* (Strayer *et al.*, 2017). However, although we have gained a good understanding of the invasion process, satisfactory explanations of invasions are still insufficient and predicting which species will become invasive and which habitat are going to be invaded remains a challenge, therefore limiting our ability to implement efficient management strategies (Moles *et al.*, 2012; Heger *et al.*, 2013).

For a long time, these questions (invasiveness and invasibility) were addressed separately, but it is now acknowledged that they should be considered together, for instance through the use of methods from community ecology (Pyšek & Richardson, 2006; Gallien & Carboni, 2017). We also know that there is no single set of traits that explains invasion success across species, as there are no simple combinations of attributes that explain habitat invasibility (Richardson & Pyšek, 2006; van Kleunen *et al.*, 2010; Gurevitch *et al.*, 2011). In fact, invasions appear to be context specific and observations are therefore linked to particular places, times, and scales (Theoharides & Dukes, 2007).

This idiosyncrasy is at least partly explained by the fact that processes underlying invasions change between habitats, stages of invasion and thus, over time. Some authors

therefore propose that, for many (plant) species, invasions may be divided into primary and secondary invasions (Fig. 4; Dietz & Edwards, 2006). During primary invasions, a species quickly increases its abundance thanks to a high propagule pressure of hybrids or preadapted genotypes that spread into mostly rich and disturbed habitats. In secondary invasions however, the species populations invade more natural habitat characterized by higher biotic resistance or harsher abiotic conditions. Secondary invasions therefore present slower rates of spread and are only possible for species that possess or gain the genetic potential to extend their ecological tolerance (Dietz & Edwards, 2006) and thus, broaden their niche (Ellstrand & Schierenbeck, 2000; Richards *et al.*, 2006; Alexander & Edwards, 2010; Gioria *et al.*, 2011; but see Petitpierre *et al.*, 2012).

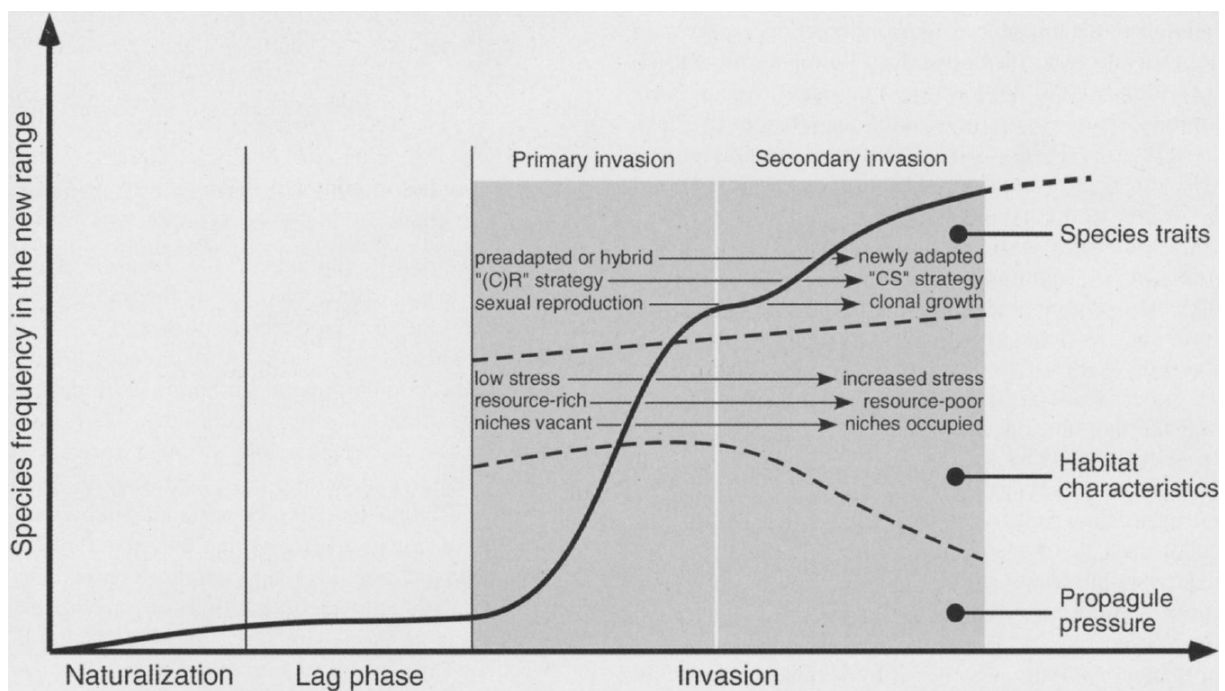


Figure 4. Conceptual representation of an invasive plant species entering its secondary phase of invasion after having colonized most directly suitable areas/habitats during its primary phase of invasion. The changing areas separated by dashed lines represent the relative importance of species traits (related to their invasiveness), habitat characteristics (related to their invasibility), and propagule pressure (promoting plant invasion) as invasion progresses. Over time changes of the important attribute of species or habitats are indicated by the arrows. This conceptual model addresses varying habitat conditions at both the local scale (where there may be a temporal overlap between primary and secondary phases) and at the regional or continental scale (e.g. latitudinal gradient, where the secondary phase of invasion is likely to be temporally separated from the primary phase). Letters C (competitor), S (stress-tolerator) and R (ruderal) refer to the CSR strategy of plant species of Grime (figure from Dietz & Edwards, 2006).

If it is heuristically convenient to depict invasions as a process involving successive stages, invasions are actually discontinuous in space and time (Pyšek & Hulme, 2005). Introductions, establishment, local and long-distance expansions are all happening simultaneously, meaning that invasions are by nature occurring at multiple spatial and temporal scales (Pyšek & Hulme, 2005; Pauchard & Shea, 2006; Theoharides & Dukes, 2007). In order to be able to fully understand invasion dynamics and predict their evolution, multiscale studies must be

undertaken. Indeed, it is likely the only way to move from idiosyncrasy to a systemic and integrated understanding of the hierarchical mechanisms that control the movements of invasive species across scales and thus their impacts. Yet, empirical multiscale studies are rare, likely because they require specific techniques and lot of time and perspectives (With, 2002; Pauchard *et al.*, 2003; Pauchard & Shea, 2006). This is why models are so often used to study the spatiotemporal dynamics of plants and animals (Levin, 1992; Pyšek & Hulme, 2005; Kueffer *et al.*, 2013), especially at large spatial scales.

Finally, it is also important to account for the fact that invasions, their pathways, their dynamic manifestations in space and time, and their underlying processes are evolving under the combined forcing of the other components of anthropogenic global change, such as land-use or climate change (Theoharides & Dukes, 2007; Walther *et al.*, 2009; Bradley *et al.*, 2010; Pyšek *et al.*, 2010; Moles *et al.*, 2012; Colautti & Barrett, 2013; Kueffer, 2017).

1.1.3. Let the fun begin: on the multiscale management of invasions

Whether we aim at preserving a certain *pristine nature* for its intrinsic value or whether we want to preserve key ecosystem functions for anthropocentric stakes, reasons to manage exotic species (especially invasive ones) do not lack. If most strategies for controlling invasions have been designed at the local scale, progresses in the awareness of the complexity of invasions and help from technological advancements (such as remote sensing or numerical modelling) have led to the development of much more comprehensive and efficient management strategies (Pauchard & Shea, 2006; Hulme *et al.*, 2008; Pyšek & Richardson, 2010).

Similarly to invasions themselves, integrative and adaptive management strategies are multiscale and vary depending on the context and stage of invasion (Pyšek & Richardson, 2010; Simberloff *et al.*, 2013). As the least problematic invasion is the one that does not happen, the first and most crucial step for effective management is *prevention* (i.e. risk assessment, information, quarantine, international bans). If introduction does occur, then *early detection* and control are acknowledged as the cheapest and most efficient ways to tackle invasive species (Wittenberg & Cock, 2001; Pluess *et al.*, 2012; Simberloff *et al.*, 2013). For such a purpose, monitoring is often essential. When early eradication was not possible or was unsuccessful, then things get far more complicated. In many cases, widespread species cannot be eradicated and should thus be contained: large scale campaigns of control should sometimes be endeavoured, but most importantly, the lower steps of the strategy (i.e. prevention and early management) must be applied and generalized at all relevant scales and locations. Efforts should be maintained through time, and monitoring and coordination among stakeholders are usually crucial to obtain satisfactory results such as preserving uninvaded areas and spatially stabilizing the problem (Fig. 3 & 5; Theoharides & Dukes, 2007; Hulme, 2009; Pyšek & Richardson, 2010; Pluess *et al.*, 2012; Simberloff *et al.*, 2013).

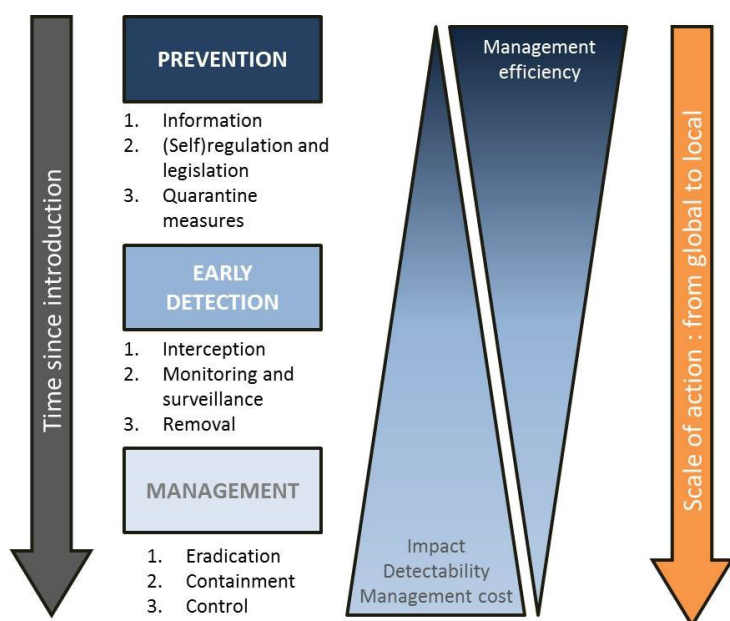


Figure 5. Management strategy against invasive species. The optimal strategy evolves with time since introduction, with management efficiency decreasing and management costs increasing with residence time and thus, with the spatial extent of invasion (inspired from Simberloff *et al.*, 2013).

Despite all the progresses that have been made, managing invasive species remains a huge species-specific challenge, and invasions are still progressing in most regions of the world.

1.1.4. The good, the bad and the ugly: an introduction to knotweeds

On the eighth day, God created Japanese knotweed and invasion biologists and said: “let them fight!”. And he laughed, and laughed, and laughed.

More seriously, in 1846, a German physicist named Phillipp Franz Balthazar von Siebold who had worked as surgeon major in a Dutch East Indies Company outpost in Nagasaki had the brilliant idea of introducing (among other things) specimens of a herbaceous plant that he named *Polygonum cuspidatum* Siebold & Zucc. Actually, dried tissues of this taxon had already been introduced in 1777 by the Dutch botanist Houttuyn who named it *Reynoutria japonica* Houtt. It was not until 1901 that somebody realized that these two names designated in fact the same plant, Japanese knotweed (syn. *Fallopia japonica* (Houtt.) Ronse Decraene). Soon after introducing Japanese knotweed in its nursery in Leiden (The Netherlands), von Siebold started to give or sell specimens throughout Europe, for the great delight of the horticultural world of this time (Fig. 6; Townsend, 1997; Bailey & Conolly, 2000). A few years later, in 1855, St. Petersburg Botanic Gardens received seeds of a plant quite similar to Japanese knotweed that they named *Polygonum sachalinense* F. Schmidt (i.e. the Sakhalin knotweed; syn. *Reynoutria sachalinensis* (Schmidt Petrop.) Nakai, and *Fallopia sachalinensis* (Schmidt Petrop.) Ronse Decraene). It had been brought back from Sakhalin island by Dr. H. Weyrich, surgeon on a ship of the Russian Navy Expedition in eastern Asian (1852-55). At the same period, others also “discovered” this plant and brought specimens in Europe. Soon, several genotypes of Sakhalin knotweeds were dispatched in many botanical gardens of Europe (Sukopp & Starfinger, 1995; Bailey & Conolly, 2000; Thiébaud & Piola, 2017).



The Great Japan Knotweed (*Polygonum cuspidatum*).
(Showing the plant in flower.)

***Polygonum cuspidatum*.**—If, instead of the formal character of much of our gardening, plants of bold types similar to the above were introduced along the sides of woodland walks and shrubbery borders, how much more enjoyable such places would be, as at almost every step there would be something fresh to attract notice and gratify the eye, instead of which such parts are generally bare, or given up to weeds and monotonous rubbish.

Figure 6. Presentation of *Reynoutria japonica* in the 1881 edition of *The Wild Garden* by William Robinson. During all the 19th century, this species was one of the most praised (and most expensive) ornamental plants that one could find. It was therefore eagerly planted in hundreds of gardens in Europe and in North America. Still, the same William Robinson wrote in 1921 that knotweed was easier to plant than to get rid of (Townsend, 1997; Del Tredici, 2017).

During the end of the 19th century and the beginning of the 20th, both knotweed taxa continued to be transported and introduced as ornamental or fodder plants (or as sand dunes stabilizers) in many temperate regions of the world: e.g. United Kingdom in 1848, France in 1853, USA before 1868, Czech Republic in 1869, Germany in 1872, Poland in 1882, Norway in 1883, New Zealand in 1935, Chile before 1960 (Patterson, 1976; Conolly, 1977; Pyšek & Prach, 1994; Bailey & Conolly, 2000; Ainsworth *et al.*, 2002; Alberternst & Böhmer, 2006; Fuentes *et al.*, 2011; Del Tredici, 2017; Holm *et al.*, 2017; Thiébaud & Piola, 2017). Soon, they managed to escape from gardens and started to spread slowly in the wild. In the meantime, when Japanese and Sakhalin knotweeds met or when they were planted together, they started to hybridize to produce the Bohemian knotweed: *Reynoutria x bohemica* Chrtek & Chrteková

(syn. *Fallopia x bohémica* (Chrtek & Chrteková) J. P. Bailey, and *Polygonum x bohemicum* (Chrtek & Chrteková) P. F. Zika et A. L. Jacobson) (Bailey & Wisskirchen, 2006; Bailey *et al.*, 2009). These three taxa form the knotweed complex (*Reynoutria* spp.; hereafter referred to as knotweeds), along with all the crosses and backcrosses between these taxa and any other related species, notably *Reynoutria japonica* var. *compacta* (Houtt.) J.P. Bailey and *Fallopia baldschuanica* (Regel) Holub (Bailey *et al.*, 2009; Bailey, 2013). Over the years, there has been many debates regarding their taxonomic identity within the *Polygonaceae* family, but recent work by Schuster *et al.* (2011) suggest that the oldest genus name, *Reynoutria*, is the most correct (but see Bailey, 2013).

It is quite difficult to distinguish the three main knotweed taxa from each other. They all produce high hollow stems with very visible nodes (hence the name: *knot-weed*) that may reach 4-5 metres in height (Fig. 7), except *R. japonica* var. *compacta* whose height does not exceed one metre (Beerling *et al.*, 1994). *Reynoutria sachalinensis* possesses large and long leaves (> 20 x 30 cm) with a cordate base and long trichomes on their abaxial surface; *R. japonica* possesses smaller leaves (10-15 cm long) with a truncate base and no visible hairs, while *R. x bohémica* displays an intermediate appearance (Zika & Jacobson, 2003; Bailey *et al.*, 2009). All knotweeds produce long creamy-white inflorescences in late-summer that are visited by numerous insects (Fig. 8; Davis *et al.*, 2018).

Figure 7. In only three months, knotweeds are able to produce stems that exceed three metres in height.



Knotweeds are gynodioecious species; i.e. they are either male-sterile (female) or hermaphrodite (Bailey, 1989; Bailey & Stace, 1992; Hollingsworth & Bailey, 2000). The sexuality and genetic structure of knotweeds' populations are complicated. All knotweed taxa can hybridize with each other, and introgression as well as polyploidization events are frequent (Mandák *et al.*, 2005; Gammon *et al.*, 2007; Grimsby *et al.*, 2007; Krebs *et al.*, 2010; Bailey, 2013; Parepa *et al.*, 2014; Park *et al.*, 2018). Consequently and unlike what was thought for a long time, we now know that knotweeds can reproduce sexually in many regions, given the presence of the right combination of taxa, sexes and ploidy levels (Bailey *et al.*, 2007; Tiébré *et al.*, 2007; Saad *et al.*, 2011). However, even when viable seeds are produced, they give birth to frail seedlings that are very sensible to competition and climatic

conditions (Bailey, 2003; Funkenberg *et al.*, 2012). This is why the expansion of knotweeds is mainly due, by far, to the dispersal of vegetative propagules (Pyšek & Prach, 1994; Barney *et al.*, 2006; Bailey *et al.*, 2009). And what a success! Knotweeds are now widespread throughout Europe and North America (Alberternst & Böhmer, 2006; Barney *et al.*, 2006), and are also present (and even locally abundant) in Chile (Saldaña *et al.*, 2009; Fuentes *et al.*, 2011), Australia (Ainsworth *et al.*, 2002), New Zealand (Howell & Terry, 2016), and in South Africa (Germishuizen, 1986).



Figure 8. The numerous inflorescences of knotweed taxa offer a source of food for pollinators in late-summer and early-autumn.

In the numerous sites invaded by knotweeds, these engineer species often induce many changes. Knotweeds possess an impressive rhizomatous system that can store large quantities of resources (Callaghan *et al.*, 1981; Price *et al.*, 2002). In spring, or following a disturbance, knotweeds can mobilise these large reserves to quickly outgrow all the other herbaceous species. In their introduced range, this advantageously fast growth associated with their allelopathic arsenal and a lack of enemies enable knotweeds to form dense monoclonal stands that can cover hundreds of square metres (Fig. 9; Barney *et al.*, 2006; Maurel *et al.*, 2013; Dommaget, 2014; Rouifed *et al.*, 2018b).

This extensive growth form enables such an efficient light interception that it usually excludes all other plant species, except when knotweeds are growing under the canopy of trees (Beerling *et al.*, 1994; Gerber *et al.*, 2008). In turn, the exclusion of native plants may affect various levels of trophic networks (Gerber *et al.*, 2008; Urgenson *et al.*, 2009). As the chemical composition of their tissues differs from that of native species, knotweeds are also associated with important modifications of soil communities and biogeochemical cycles (e.g. Aguilera *et al.*, 2010; Dassonville *et al.*, 2011; Claeson *et al.*, 2014). In a review of their environmental impacts however, Lavoie (2017) reminds us that if some taxa are negatively impacted by knotweeds (e.g. soil bacteria, most arthropods and gastropods, some birds and amphibians), other species benefit from their presence (e.g. most soil fungi, detritivorous arthropods, aquatic shredders and some birds). Recent work also showed that sites invaded

by *R. japonica* displayed a higher diversity of pollinators than uninvaded sites (Davis *et al.*, 2018). Therefore, although knotweeds undeniably modify their immediate environment, assessing their global effects on ecosystems is more complicated than it seems (Lavoie, 2017; Davis *et al.*, 2018).

Figure 9. Large knotweed monocultures of this size or even larger are quite frequent in many regions of Europe and North America (here, in Lais county, Ireland).



Nevertheless, in addition to their effects on biodiversity and the functioning of ecosystems, knotweeds are associated with several impacts related to anthropic activities. Along roads or railways, knotweeds frequently cause security problems by reducing visibility. In such places, or along rivers, knotweeds also cause accessibility problems for users, and/or impede the regular maintenance of certain land or infrastructures (Beerling, 1990; Cottet *et al.*, 2015). It seems that forest managers are increasingly concerned by the presence of knotweeds inside or around their plots, as they fear that knotweeds may profit from clearcuttings to gain dominance (Dommanget *et al.*, 2016). When people can identify knotweeds, they also negatively affect the landscape perception of users (Rouifed *et al.*, 2018a). In some cases, knotweeds can also damage infrastructures (Fig. 10; Beerling, 1991; Shaw & Seiger, 2002), but mostly by widening already existing cracks (Fennell *et al.*, 2018). Finally, despite the fact that numerous sources state that knotweeds favour flood hazards and although they probably have an effect on hydrogeomorphological processes on heavily invaded rivers (van Oorschot *et al.*, 2017), these hypotheses have never been properly tested (Lavoie, 2017).



Figure 10. Regenerating ramets of knotweed growing through a freshly resurfaced road in the French Alps near Grenoble. As no knotweeds grew there before the surfacing works, fragments of the plant must have been brought by the heavy equipment used for the works.

Due to the various problems they cause, knotweeds have been the target of management operations for more than a century (Bailey & Conolly, 2000). Nevertheless, despite tenacious efforts, countless studies, one book and at least three literature reviews (e.g. Child & Wade, 2000; Kabat *et al.*, 2006; McHugh, 2006; Bashtanova *et al.*, 2009), knotweeds remain stubbornly persistent and close to impossible to eradicate once they are established unless investing very high amount of time and/or money (with no guarantee of results). Fire, liquid nitrogen, various combinations of chemicals, microwaves, repeated mowing, shredding or crushing, biological control, geotextiles, excavation and more: a small tour on the internet or in some references dealing with knotweeds' management illustrates the multitude of attempts made to control them and explains the fact that knotweeds are usually perceived as "unmanageable" (Rouified *et al.*, 2018a). It also highlights the contradictions on management recommendations and the absence of consensus about how knotweeds should be controlled (Delbart *et al.*, 2012; Robinson *et al.*, 2017). The impacts of knotweeds and the difficulty to control them have earned some of them (i.e. *R. japonica*) a place on the list of the worst plant invaders in the British Isles (Environment-Agency, 2013) as well as on the list of worst invaders in the World (Lowe *et al.*, 2000).

The resilience of knotweeds is largely linked to their impressive regeneration abilities (Callaghan *et al.*, 1981; Seiger & Merchant, 1997; Child, 1999). Gifted with a large phenotypic plasticity possibly of epigenetic origin (Richards *et al.*, 2012; Gillies *et al.*, 2016), knotweeds exhibit a high resource-use efficiency that enables them to quickly accumulate reserves in various conditions (Palmer, 1994; Aguilera *et al.*, 2010; Parepa *et al.*, 2013).

Given the difficulty to eradicate knotweeds at the local scale, a change of paradigm in the way we deal with their invasion is increasingly acknowledged (Delbart *et al.*, 2012; Cottet *et al.*, 2015; Clements *et al.*, 2016). Instead of persisting in fighting a lost battle, efforts should possibly be redirected toward preventing further knotweeds' expansion at different spatial scales, notably in order to protect still preserved environments. Considering the much higher cost-efficiency of early detection and control, improving our abilities to predict and/or detect knotweeds appears to be paramount (Hulme, 2003; Schifflerthner & Essl, 2016). Additionally, spatial prioritisation may also be a way to improve our ability to control knotweeds' population and their expansion (Meier *et al.*, 2014; Perry *et al.*, 2016).

For all these purposes, it seems that getting a thorough understanding of the spatial and temporal dynamics of knotweeds (or any other invasive species) at various scales is required (Collingham *et al.*, 2000; MEEM, 2017). However, despite decades of study and hundreds of papers on knotweeds, only few studies directly addressed this question directly, and many uncertainties remain (Pyšek & Hulme, 2005; Tiébré *et al.*, 2008; Navratil *et al.*, 2018). Even the apparently simple question of the environmental niche of knotweeds is not quite resolved while being of prime importance to predict the dynamics of any plant species. Knotweeds are most frequently found in open, rich and/or disturbed habitats such as transport infrastructures (i.e. roads, highways, railways), riparian areas, and derelict or industrial lands (Tiébré *et al.*, 2008; Rouified *et al.*, 2014; Sołtysiak & Brej, 2014). However, we know that floods and anthropic activities (e.g. earth movements for public works) are likely the main dispersal vectors of knotweeds (Pyšek & Prach, 1994; Barney, 2006). Therefore, the higher

abundance of knotweeds in these types of habitats may possibly be a spurious correlation. In fact, knotweeds are known to possess a large environmental tolerance (Fig. 11) enabling them to grow in a large array of edaphic conditions (Palmer, 1994; Barney *et al.*, 2006) and light availability (Beerling *et al.*, 1994; Dommanget *et al.*, 2016; Wilson *et al.*, 2017). Therefore, it is difficult to assume that knotweeds are truly subordinated to open, rich and/or disturbed environments only (Tiébré *et al.*, 2008; Clements & DiTommaso, 2012).



Figure 11. Knotweeds are famous for their environmental tolerance and their resilience that enables them to grow in places as diverse as closed forests (a), roadsides (b), rip-raps (c), dark cold-rooms (d), railway electrical cabinets (e), or even bridge columns (f).

1.2. OBJECTIVES OF THIS THESIS WORK

Understanding the interactions between ecological and scalar processes is one of the greatest challenges in ecology (Allen & Starr, 1982; Levin, 1992; Pauchard & Shea, 2006). We could add that to get insights on a process, one must look into the patterns it creates. As Simon Levin said in his famous lecture in the honour of Robert MacArthur, “understanding patterns in terms of the processes that produce them is the essence of science, and is the key to the development of principles for management” (Levin, 1992).

These considerations are particularly important in invasion ecology. The *invasion dynamics* (or spatiotemporal dynamics) of a clonal plant species could be defined as the movements in space through time of the biological units of one or several of its organizational levels; i.e. modules, ramets, clonal fragments, genets, populations, metapopulations, and the whole species. We have mentioned that the invasion dynamics of a species are controlled by a hierarchy of processes operating at various spatiotemporal scales (Pyšek & Hulme, 2005; Pauchard & Shea, 2006; Theoharides & Dukes, 2007). Furthermore, it appears that the levels of this hierarchy are not independent but are influencing each other (Allen & Starr, 1982; Wiens, 1989; Levin, 1992; Theoharides & Dukes, 2007). Consequently, to fully understand the processes that drive the spatiotemporal dynamics of a species at every level of this hierarchy, one must therefore look at the patterns created at all relevant spatiotemporal scales (Wiens, 1989; Pyšek & Hulme, 2005; Pauchard & Shea, 2006; Gurevitch *et al.*, 2016). The ambition of such profound insight is high, but it matches the stakes: apprehending these dynamics and their causes is getting to understand where current impacts are and where future impacts will be, as well as knowing where and how to act to limit or reverse these impacts (Pauchard & Shea, 2006; Pyšek & Richardson, 2010). This is likely true for invasive clonal species such as knotweeds.

In the light of these elements and considering that our ability to predict knotweeds' invasion dynamics remain limited, we tried to highlight **what the main drivers of the spatiotemporal dynamics of Asian knotweeds across scales are, and how their management can benefit from a deeper understanding of these dynamics?**

Of course, it would be naïve to think that one could unravel all the secrets of knotweeds' expansion (or regression) across all possible scales in the duration of a single Ph.D. The spread of knotweeds likely occurs on countless environmental gradients that possibly differ in terms of steepness and heterogeneity, biological composition, anthropic development, knotweed taxa composition, history and time since introduction. Properly investigating this multitude of situations would require means that probably exceed by far the financial or human capacities of any scientific lab. More modestly, the idea behind this thesis work was to unblock some key fundamental or methodological points related to the study of knotweeds' invasion dynamics at different spatial scales to facilitate the acquisition of a more insightful comprehension of their movements in space and time and link it to management perspectives (Fig. 12).



Figure 12. Illustration of some (non-exhaustive) questions related to the dynamics of knotweeds in space and time at different scales. The various shades of green represent the environmental heterogeneity relevant at each scale. Each of these questions can be potentially useful for knotweed management: (1) what is the probability of survival of knotweed juveniles in these two habitats (useful for prediction or restoration)? (2) How is the clonal growth of knotweeds affected by environmental heterogeneity (useful to eventually contain or orientate the growth of knotweeds)? (2*) How does this growth change as clonal fragment become older (useful to know how far clonal fragments can go)? (3) Is this growth different for stands composed of multiple individuals (useful to eventually contain or orientate the growth of knotweeds)? (4) What is the origin of these knotweed individuals (useful to control dispersal vectors)? (5) How are these populations spreading (useful for prediction or to prioritize management)? (6) How fast will this isolated population be able to interact with other populations (useful to prioritize management)? (7) What is the invasibility of these habitats (useful for monitoring, early control or restoration)? (8) Are there more chances to find knotweeds close to urban areas or roads (useful for prediction)? (9) Are these populations ever in contact (useful to identify dispersal vectors)? (10) From where does this population initially came (useful to identify potential preserved areas)? (11) What are the demographic properties of all these populations (useful for prediction)? (12) How can we monitor these populations (useful for early detection or to assess the effects of control operations)?

More precisely, in the following chapters, we have tried to:

- 1- Highlight how young clonal fragments of knotweed (only *R. japonica*) adapt to varying environmental conditions during their establishment phase (i.e. mostly questions 1 and 2 in figure 12);

- 2- Examine what explains the expansion or regression of knotweeds' stands (possibly composed of several fragments of knotweeds) along an elevational gradient to get insights on the unexpected niche width of these taxa (i.e. mostly questions 2, 2*, 6 and 7 in figure 12);
 - 3- Develop a procedure to accurately detect and monitor knotweeds through remote sensing at two different spatial resolutions and in different context of environmental heterogeneity to contribute to the development of tools for a time-efficient analysis of their spatiotemporal dynamics in the landscape (i.e. question 12 in figure 12);
 - 4- Provide an up-to-date synthesis of the knowledge on knotweeds' invasions dynamics by carefully reviewing the literature for direct and indirect evidences on their presence and movements from the ramet to the regional/country scale and highlight potential knowledge gaps and future research perspectives (i.e. all questions in figure 12 and more).
- This latter chapter-article will consequently be used as the Discussion of the thesis as it will confront the other chapters with the current knowledge on the spatiotemporal dynamics of knotweeds across scales and, hopefully, expand their conclusions.

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– CHAPTER TWO: ESTABLISHMENT AND INITIAL CLONAL GROWTH –



A first logical step to gain a thorough understanding of the invasion dynamics of knotweeds across scales is perhaps to investigate how knotweeds' stands are created and how they initially develop. Behind any large scale invasion of knotweeds, there is an establishment event and a subsequent clonal growth. Besides, the vigour and resilience of knotweeds are probably also strongly linked to their clonal abilities. Gaining insights into how these processes occur, and how they will be affected by the various environmental conditions knotweeds will encounter during their life appears to be important for predicting the evolution of an invaded site, understanding how the cover of stands affect native ecosystems, and possibly highlighting ways to influence the lateral expansion of these plants.

In this chapter, we present an article that investigates some the fascinating aspects of knotweeds' clonal behaviour.

2. INSIGHTS INTO THE CLONAL GROWTH STRATEGIES OF *REYNOUTRIA JAPONICA* UNDER VARIOUS ENVIRONMENTAL CONDITIONS AND PERSPECTIVES FOR MANAGEMENT

(Article in preparation for submission in *Plant Species Biology*)

2.1. INTRODUCTION

Clonality is an attribute that is frequently associated with plant invasiveness (Lloret *et al.*, 2005), and many of the most invasive plants in the world are clonal (Lowe *et al.*, 2000; Liu *et al.*, 2016). This is unsurprising as the highly plastic modular growth form of clonal plants release them from many constraints related to sedentariness. In clonal plants, resource-acquiring structures located on ramets (potentially autonomous physiological individuals) such as leaves and root tips are projected into the environment by *spacers* (Hutchings & de Kroon, 1994): usually stolons or rhizomes. If ramets are fixed, whole *clonal fragments* (physical individuals) can spread laterally and may exhibit a large mobility (Oborny & Cain, 1997; Zobel *et al.*, 2010). By plastically changing the length, direction and/or number of spacers, clonal plants are able to exhibit complex behaviours such as precision foraging and selective ramet placement, escape strategies, or division of labour with ramets specialization (de Kroon & Hutchings, 1995; Hutchings & Wijesinghe, 1997; Gao *et al.*, 2012; Oborny *et al.*, 2012). Clonality also enables survival and persistence of populations in absence of sexual reproduction (Eriksson, 1997), rapid cover and dominance of invaded sites (Herben & Hara, 1997; Pyšek, 1997), and, through clonal integration, the exchange of assimilats and information between connected ramets to reduce resource shortages and mitigate the effects of stresses and disturbances (Jónsdóttir & Watson, 1997; Liu *et al.*, 2016). Out of these many advantages, some have been shown to be particularly associated with invasiveness such as high root foraging abilities or clonal integration (Song *et al.*, 2013; Keser *et al.*, 2014). Yet, many unknowns remain regarding the link between clonality and invasiveness, and the study of clonal invaders represent a key stake for many fundamental and applied ecological questions (Liu *et al.*, 2016; Yu *et al.*, 2016).

At the local scale, since the performances and impacts of invasive clonal plants are often directly related to their clonal growth characteristics (e.g. architectural traits, lateral growth rate, ramet density, clonal integration, growth strategies), understanding clonal growth patterns and strategies is of prime importance to improve management strategies. This is why the clonal growth dynamics of many highly problematic clonal invaders have been the subject of extensive research over the years: e.g. *Phragmites australis* (Amsberry *et al.*, 2000; Bellavance & Brisson, 2010; Douhovnikoff & Hazelton, 2014), *Carpobrotus edulis* (Roiloa *et al.*, 2010; Roiloa *et al.*, 2013), *Solidago spp.* (Hartnett & Bazzaz, 1983; Stoll *et al.*, 1998; Jakobs *et al.*, 2004).

On the other hand, despite being listed as one of the worst invasive plant in the world (Lowe *et al.*, 2000), Japanese knotweed (*Reynoutria japonica* Houttuyn) present clonal growth

dynamics that are still poorly understood. Capable of an early and rapid growth by remobilizing resources stored in its rhizomes, *R. japonica* often forms dense monoclonal stands that exclude many native species and may be an important nuisance for various anthropic activities (Beerling *et al.*, 1994; Child & Wade, 2000). Gifted with incredible regeneration abilities, populations of *R. japonica* are extremely difficult to control (Child & Wade, 2000; Delbart *et al.*, 2012) and have, mainly by vegetative spread, successfully colonized most temperate regions of the world (Beerling *et al.*, 1994; Alberternst & Böhmer, 2006). In its native range, in the very specific environment of the high elevation volcanic deserts of Japan, several studies have highlighted that clonal fragments of *R. japonica* var. *compacta* expand by reiterating a fixed pattern of sympodial rhizome growth (at the end of which clumped ramets are produced) with important clonal integration among ramets of different size to avoid asymmetric competition (Suzuki, 1994; Adachi *et al.*, 1996a, b). In its introduced range however, investigations on the clonality of *R. japonica* have mainly focused on its regeneration capacities (e.g. Bímová *et al.*, 2003), or on the source of these capacities (Price *et al.*, 2002). Two modelling studies also tried to understand the development of *R. japonica*'s clonal fragments by following growth rules derived from the Japanese studies. Yet, they recognized that their results were subjected to serious restrictions due to the lack of quantitative data on the variability of clones' growth and demography in various environmental conditions (Smith *et al.*, 2007; Dauer & Jongejans, 2013).

Clones of *R. japonica* are mainly heliophilous, but closed-habitats such as forests may still be colonized either directly from vegetative propagules, or from the lateral expansion of surrounding populations (Beerling *et al.*, 1994; Tiébré *et al.*, 2008). Closed-habitats diminish their performances and the restauration of competitive native species is increasingly used to control *R. japonica*'s populations (Dommanget *et al.*, 2013). Still, mowing remains the main control technique used against *R. japonica* in many regions, either on the whole surface of stands or on part of it: e.g. when on roadsides or at the border between two properties (Delbart *et al.*, 2012; Schiffléithner & Essl, 2016). Chances are that the clonal dynamics of *R. japonica* individuals vary substantially between the various possible combinations of growing conditions mentioned here: i.e. whole clonal fragments (or part of it) growing in full-light or under a closed canopy, and being mowed or not. For instance, some authors report that shaded clones usually display a lower ramet density than the ones growing in open areas (Beerling, 1991; Dommanget *et al.*, 2019) or that, conversely, mowing increases ramet density and favours stands' expansion (Beerling, 1990; Child & Wade, 2000).

In order to start filling the gap in our understanding of the invasion dynamics of *R. japonica* that constitutes its clonal growth, we designed a mesocosm experiment to explore how the development and expansion of young clonal fragments is affected by homogeneous or heterogeneous conditions of stress (shade) and disturbance (mowing). The idea was to highlight potential growth strategies and trade-offs when faced with more or less favourable habitats, and investigate how these adaptations can be relevant to improve the management of *R. japonica* by mowing/cutting or by ecological restoration of competitive species. We hypothesized that: i) a homogeneously high light availability would favour a clumped aggregation of ramets while a homogeneous shade would favour a more scattered distribution of aerial shoots, two growth forms respectively known as *phalanx* and *guerilla*

(sensu Lovett Doust, 1981); ii) mowing will lift the apical dominance of ramets over their nearby axillary buds, therefore favouring a higher rhizome branching frequency and ramet density than in un-disturbed *phalanx* clones; and iii) individuals that have a part of their clonal fragments submitted to a stress (shade) or a disturbance (mowing) will try to 'escape' these less favourable habitats by investing more in the growth of their parts growing in sunny and undisturbed areas.

2.2. MATERIALS AND METHODS

2.2.1. Biological material

In April 2017, rhizomes belonging to a single *R. japonica* individual have been manually excavated. The plant was located outside the village of Cholonge (1061 m a.s.l.; 45°00'N – 5°79'E), in the French Alps. This individual was chosen because it was growing in an open and unmanaged site. This was an important prerequisite since we wanted to avoid that the juveniles born from the rhizome fragments display a particular adaptation to stressful or disturbed conditions due to transgenerational inheritance (Latzel & Klimešová, 2010; Latzel *et al.*, 2016).

Back to our lab, the rhizomes were washed and cut to obtain homogenized fragments with the same approximate weight and number of nodes. The thirty most identical fragments were selected and then bagged and stored in a cold room before the beginning of the experiment. These fragments had a mean weight of 16.44 g (\pm 0.85 g) and a mean number of nodes of 8.06 (\pm 2.46).

2.2.2. Experimental design

The mesocosm experiment was conducted in an experimental nursery of the French National Forest Office (ONF) located in Guéméné-Penfao, Brittany (France). The area is characterized by mean monthly temperatures ranging from 7.9 to 16.4°C, and 694 mm of mean annual precipitations (data from Rennes meteorological station; www.meteofrance.com).

The experimental design was composed of five treatments with six replicates each. The idea was to submit *R. japonica* individuals to various homogeneous or heterogeneous habitats in order to see what growth type structures and trade-offs they would display to adapt to these environments. Therefore, each plant would grow in pots divided into two *habitat patches*. These habitat patches were identical for the homogeneous treatments (i.e. *light* (L), *mowing* (M), or *shade* (S)) and different for the heterogeneous one (i.e. *half-light* – *half-mowing* (LM) or *half-light* – *half-shade* (LS); Fig. 1).

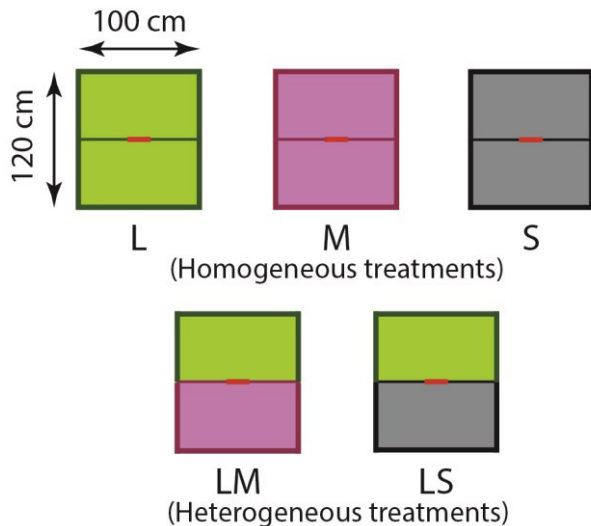


Figure 1. Experimental design. The different colours represent the various treatment modalities: green (un-shaded and un-mowed habitat), pink (un-shaded but mowed habitat) and grey (shaded but un-mowed habitat). Each of these five different treatments had six replicates. The red segments represent the position of the rhizome fragments that were planted.

In preparation of the experiment, thirty rainwater tanks of ca. 1000L (120 x 100 x 116 cm) were “opened” and changed into pots by cutting and removing their top-wall. The pots were filled with a 15 cm layer of gravels (0–32 mm) to facilitate water drainage (all pots had an outlet pipe), and approximately 100 cm of a certified substrate composed of 70% river sand, 15% loam and 15% compost. *Shade-boxes* were placed atop the pots meant to harbour the replicates of the treatments involving shade (i.e. S and LS). These shade-boxes consisted of 3 m poles planted in the pots and covered with a shading-net that filtered around 80% of light. All pots were then dispatched on a flat area. Their location and orientation was randomly chosen in such a way that each replicate of a given treatment had a different orientation than the other five replicates. To avoid the effect of projected shadows caused by the tall shade-boxes, pots were placed with 4 m intervals between them in every direction.

In early May 2017, the thirty rhizome fragments were randomly assigned to one of the pots. They were buried two centimetres below the surface in the middle of the pots, orthogonally to the greater length of those. This position coincided with the limit between the two habitat patches of the pots (Fig. 1). In the mowed habitats (i.e. M and LM), the aerial shoots of ramets were manually clipped and exported every time they reached approximately 25 cm in height. This resulted in three *mowing* events during the first vegetative season, and one during the following spring shortly before the end of the experiment. This mowing frequency was chosen because it reflects the regular management along many French roads and railways. Throughout the experiment, pots were weeded regularly and water availability was maintained thanks to a multi-point dripping irrigation system. We also checked for potential differences in air temperature and soil humidity using ten TMS-4 data-loggers (www.tomst.com) randomly placed in treatments’ modalities, left two weeks, and moved to another random replicate of the same modality. Additionally, the randomized placement and orientation of all the pots was reshuffled in July 2017.

2.2.3. Harvest and measurements

Before each mowing event, the number of ramets in each habitat patch was monitored. We decided to stop the experiment when ramets began to reach the edges of pots, in order to minimize the *obstacle-effect* on the clonal architecture of the plants.

At the end of June 2018, aerial shoots of all habitat patches were counted before being cut and oven-dried during 48h at 100°C to measure their biomass. We then carefully excavated the *R. japonica* individuals, using mostly our hands in order not to break fragile rhizomes and buds, and to extract rhizomatous systems as intact as possible. Only roots were intentionally cut in order to facilitate extraction as our hypotheses were unrelated to the root systems. We then marked the position of the separation line between the two habitat patches on each rhizomatous system before “washing off” the dirt with an air compressor and brushes. Rhizome and spacer length, branching frequency, and the number of axillary and basal buds that were growing in each habitat patch were measured. Finally, we also measured rhizome biomass with the same method as for aboveground organs.

2.2.4. Statistical analysis

Prior to analyses, data were explored and prepared following the protocol of Zuur *et al.* (2010).

In this study, we performed two types of analysis. At the scale of pots, we were interested in the effect of different type of habitats (our treatments) on variables characterizing *R. japonica*'s growth form and strategies: i.e. biomass (aboveground, rhizomatous and total biomasses), cumulated rhizome length, specific spacer length (length of a spacer per unit of biomass), number of aerial shoots, and branching frequency (calculated as the number of rhizome branches per unit of rhizome length). For that purpose, we performed ANCOVAs with type II Sums of Squares and used the weight and number of nodes of the rhizomes that were initially planted as covariates. For multiple comparisons, we used pairwise *t*-tests using Holm-Bonferroni corrections to control for familywise error rates. At the scale of habitat patches (only for the heterogeneous treatments), variations in the same dependent variables were investigated but using mixed ANOVAs with *pots* as a random effect (Rutherford, 2011). Post-hoc tests were performed using Tukey's HSD test to account for possible violations of sphericity. Note that we also wanted to study potential differences in the number of buds between treatments as evidence of habitat selection, but we observed during harvest that *R. japonica* produces a bud at each node regardless of the treatment, impeding conclusions to be made.

All analyses were performed with R version 3.5.2 (R-Development-Core-Team, 2018).

2.3. RESULTS

In order to avoid so-called *data dredging*, we reserved the use of statistical tests on the variables of importance for our working hypotheses. Therefore, some of the following results are solely presented for the sake of observation.

2.3.1. General observations, biomass production and spatial exploration

All the rhizomes that we planted at the beginning of the experiment gave birth to clonal fragments that survived throughout the 13 month of the experimentation. As expected, most of the measured traits related to clonal growth presented a high variability (Table 1; Fig. 2 to 6). Interestingly, most the clones have been seen producing flowers during their first growing season except those of the entirely mowed treatment (M).

Table 1. Summary statistics of some descriptive variables measured across all treatments.

	Maximum spacer length (cm)	Mean spacer length (cm)	Cumulated rhizome length (cm)	Mean rhizome length (cm)	Number of rhizome branches	Number of buds	Number of aerial shoots	Aboveground dry biomass (g)	Rhizomatous dry biomass (g)	Total dry biomass (g)
Mean	56,07	30,59	599,2	16,65	24,6	230,42	23,97	499,45	207,04	706,49
Standard deviation	29,22	24,55	519,03	6,94	24,4	159,3	13,25	404,48	200,8	591,5
Median	53,25	23,27	484,7	16,32	17,5	220,5	22,5	325,5	98,38	394,52
Minimum	17,1	1	38,9	3,367	1	19	5	1,21	9,01	10,22
Maximum	112	92,5	2113	29,18	97	638,92	55	1221	708,66	1902,66

Unsurprisingly, individuals growing in full light (L) exhibited higher total biomass production, closely followed by the clones that were only partially mowed (LM) while entirely mowed clones (M) produced only very little biomass (Fig. 2a). With the exception of the pairs L-LM ($t = 1.532$, $p = 0.145$) and LM-LS ($t = 1.383$, $p = 0.096$), all the differences in mean *total biomass* were significant: L-M ($t = 3.792$, $p < 0.001$); L-S ($t = 3.036$, $p < 0.001$); L-LS ($t = 5.332$, $p = 0.005$); M-S ($t = 2.882$, $p < 0.001$); M-LM ($t = 3.715$, $p < 0.001$); M-LS ($t = 3.41$, $p < 0.001$); S-LM ($t = 4.129$, $p < 0.001$); S-LS ($t = 2.508$, $p = 0.013$). For the homogeneous treatments, the hierarchy of differences remained the same for aboveground and rhizomatous biomasses (data not shown). On the other hand, replicates of the LM treatment had significantly higher rhizomatous biomasses than those of the LS treatment ($t = 2.379$, $p < 0.01$), but no differences were found for aboveground biomass (Fig. 2b and c). Among the heterogeneous treatments, subtle differences appeared between the favourable habitat patches (i.e. *light* patches in treatments LM and LS) and the other halves of the pots (Fig. 2b and c), even though the only significant difference was between the mean aerial biomasses of the LM treatment's habitat patches ($t = 3.491$, $p < 0.001$).

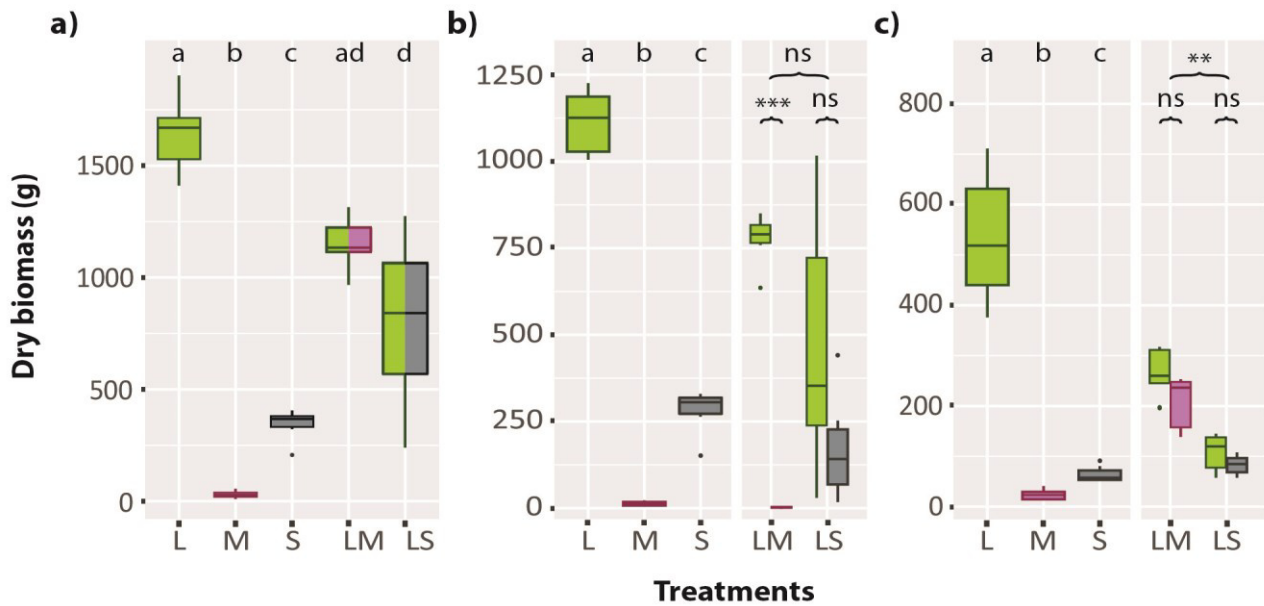


Figure 2. Differences in total dry biomass (a), aboveground biomass (b) and rhizomatous biomass (c) between the L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments. For (a) and homogeneous treatments in general, all treatments were tested together: treatments not sharing the same letter were significantly different at $p < 0.05$; for (b) and (c) however, homogeneous (L, M, and S) and heterogeneous (LM and LS) were tested separately (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant).

The spatial exploration of soil, as measured by the *cumulated rhizome length*, also showed interesting patterns (Fig. 3). Difference between the mean *cumulated rhizome length* of treatments L and LM, S and LS, or between the habitats patches of the heterogeneous treatments were insignificant.

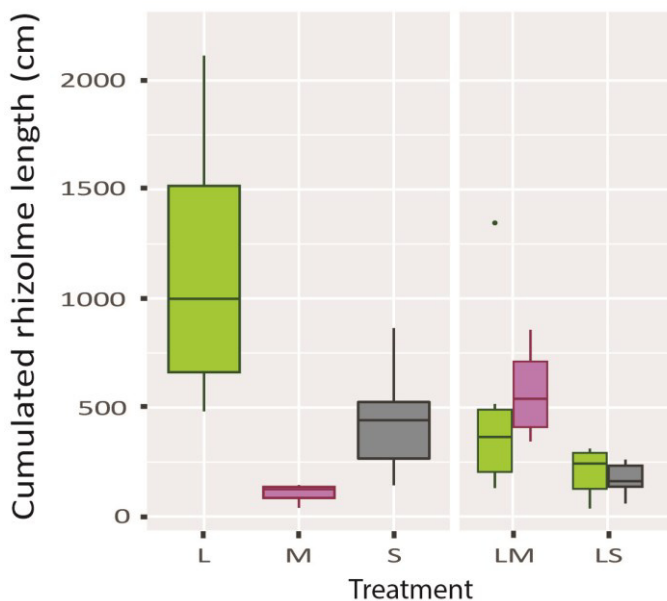
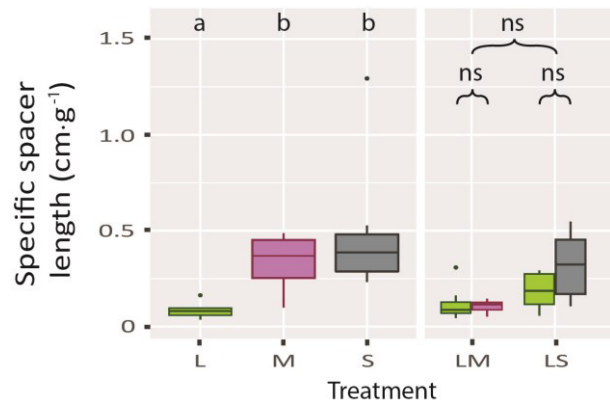


Figure 3. Differences in cumulated rhizome length between the L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments.

2.3.2. Spacer traits and ramet distribution

Individuals of *R. japonica* growing in full light (L) had significantly lower *specific spacer lengths* than clones growing in a shaded habitat (S; $t = 4.361, p < 0.001$) or than entirely mowed individuals (M; $t = 3.005, p < 0.025$). Despite a slight trend of increased *specific spacer length* in the shaded habitat patches of the LS treatment, no significant differences were found within or among heterogeneous treatments (Fig. 4).

Figure 4. Differences in specific spacer length between the L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments. Homogeneous and heterogeneous treatments were tested separately. For the former, treatments not sharing the same letter were significantly different at $p < 0.05$ while for the latter: ns = not significant.



On the other hand, individuals growing in the entirely shaded environment (S) produced less *aerial shoots* than the clones in the L ($t = -7.327, p < 0.001$) and M treatments ($t = -8.23, p < 0.001$), and there was no differences between the latter two ($t = 0.276, p = 0.89$). Interestingly, the un-mowed habitat patch of the LM treatment displayed significantly more *aerial shoots* than the mowed habitat patch ($t = 2.623, p = 0.015$; Fig. 5).

Finally, clones of the L treatment had in average a significantly higher *rhizome branching frequency* than the clones of the S treatment ($t = -2.686, p = 0.032$), but not than the entirely mowed clones (M; $t = 0.393, p = 0.267$). The latter had however a higher mean for that variable than the shaded clones (S; $t = -3.425, p = 0.011$). Here again, no significant differences were found between the habitat patches of the heterogeneous treatments LM and LS (Fig. 6). Interestingly, un-mowed halves of the LM treatments had a seemingly higher branching frequency than mowed ones, therefore exhibiting a reverse pattern compared to the homogeneous treatments L and M.

2.4. DISCUSSION

Despite its importance for understanding and managing the local invasion dynamics of *R. japonica*, the clonal growth of this invasive species and its variations under various environmental conditions have been widely understudied (Smith *et al.*, 2007; Bashtanova *et al.*, 2009). The observations and data presented in this study represent, to the best of our knowledge, the first quantitative assessment of the clonal dynamics of *R. japonica* in various homogeneous or heterogeneous habitats.

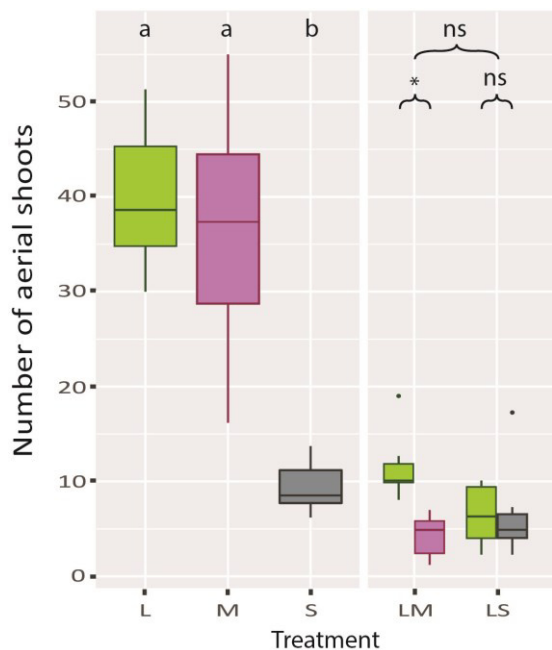


Figure 5. Differences in number of aerial shoots between the L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments. Homogeneous and heterogeneous treatments were tested separately. For the former, treatments not sharing the same letter were significantly different at $p < 0.05$ while for the latter: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant.

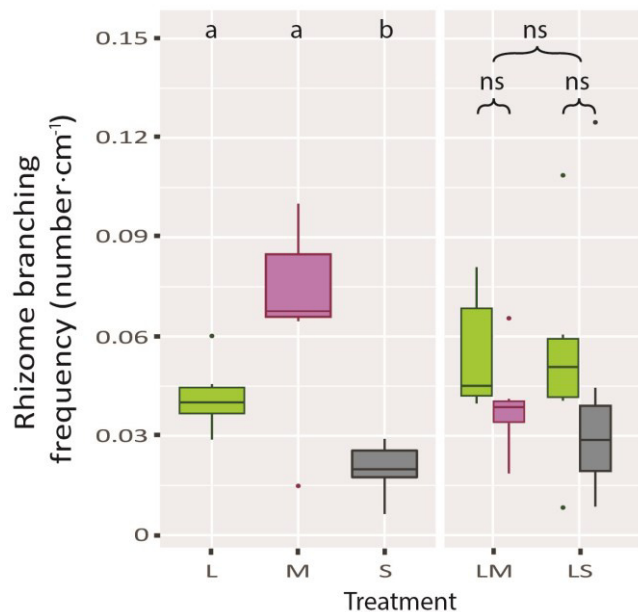


Figure 6. Differences in rhizome branching frequency (measured as the number of branches per unit of rhizome length) between the L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments. Homogeneous and heterogeneous treatments were tested separately. For the former, treatments not sharing the same letter were significantly different at $p < 0.05$ while for the latter: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant.

2.4.1. Clonal growth forms and strategies

Our results suggest that *R. japonica* can adapt to the quality of its habitat thanks to plasticity in various vegetative growth traits. In accordance with our first hypothesis, *R. japonica* adopted a phalanx growth form when growing in a homogeneously illuminated habitat by aggregating many ramets separated by short spacers. Conversely, when growing under heavy shade, the clones only presented a few ramets separated by long spacers, typical of a guerilla growth form (Fig. 4 and 5). As these two growth forms were associated with different specific spacer lengths and rhizome branching frequencies (Fig. 4 and 6), then they likely stemmed from differing clonal growth strategies and not only from differences in the vigour of clones.

Shaded clones invested proportionally more resources in the horizontal exploration of their habitat than the clones growing in full light. It is therefore possible that, in shaded environments such as a forest understorey, *R. japonica* display an *extensive foraging* strategy to increase the chances of placing ramets in sunflecks or to escape this less favourable habitat (cf. Lovett Doust, 1981; Slade & Hutchings, 1987a), as has been frequently reported for other species (Slade & Hutchings, 1987b; de Kroon & Hutchings, 1995; Xie *et al.*, 2014). On the other hand, in a homogeneously luminous environment, *R. japonica* seems to adopt a *space-consolidation* strategy (sensu de Kroon & Schieving, 1990). In this exploitative strategy, phalanx clones multiply their ramets by increased branching frequency in order to

monopolize resources and limit interspecific contacts (Lovett Doust, 1981; de Kroon & Schieving, 1990; Herben & Hara, 1997; Gough *et al.*, 2001).

In theory, phalanx species should have a slower lateral expansion rate than guerilla species (Lovett Doust, 1981; Schmid, 1986). Yet, Figures 2c and 3 show that *R. japonica* grew faster and explored more soil volume in 13 month when cultivated in full light than under shade. This is consistent with observations made on cultivated *R. japonica*'s stands (i.e. composed of several competing clonal fragments) that expanded faster and further in two seasons when grown alone than when planted in mixture with a high density of *Salix viminalis* cuttings (Dommanget *et al.*, 2019). In both cases, this difference is certainly explained by the higher vigour of clones growing in full light compared to shaded ones. Still, theory does not tell if the differences in lateral growth rates between phalanx and guerilla individuals should be constant over time or not. It could be that, in order to operate an efficient spatial pre-emption against potential competitors, the phalanx *R. japonica*'s clones have a quick initial expansion rate for a while followed by a (gradual or steep) deceleration as clones get stronger and more dominant and as their chances of being excluded decline. In the long term however, guerilla clones could perhaps expand further (to escape) or display a higher clonal mobility than phalanx ones. More long-term empirical studies are needed to verify these assumptions and more generally, to assess the differences in lateral growth rates between clonal fragments of *R. japonica* growing in differing environments as no data actually exist on the matter.

Against our expectations, the average ramet densities and branching frequencies of entirely mowed clones (M treatment) were not significantly higher than those of the illuminated and un-mowed ones (L treatment), despite interesting trends. Moreover, entirely mowed individuals had an overall very low spatial expansion. This discrepancy between our hypothesis and observations is likely due to the intensity of the mowing events. As these clones had to cope three times with the total destruction of their aerial organs during their first growing season, their biomass production and spatial exploration must have been strongly constrained (Fig. 2 and 3), hence limiting our ability to properly observe their clonal growth patterns. The intellectually appealing hypothesis stipulating that mowing breaks the apical dominance of *R. japonica*'s aerial shoots and thus favours rhizome branching and the lateral expansion of clonal fragments (cf. Beerling, 1990; Bashtanova *et al.*, 2009) consequently requires further study.

Stands of *R. japonica* frequently grow in habitats that are not homogeneously illuminated and/or mowed such as roadsides, semi-natural riverbanks or forest edges (Beerling *et al.*, 1994; Tiébré *et al.*, 2008; Martin *et al.*, 2019). In those, we may expect the clones to embrace particular adaptations to cope or to avoid the effect of less favourable areas. Unfortunately, our clones grown in heterogeneous conditions did not demonstrated many significant differences between favourable (illuminated and undisturbed) and unfavourable (shaded or mowed) habitat patches for most studied traits. It could be that *R. japonica* is unable to select a preferential habitat and that it does not attempt to escape through directional growth (e.g. Evans & Cain, 1995; Sampaio *et al.*, 2004) or selective placement of ramets (e.g. de Kroon & Hutchings, 1995; Wijesinghe & Hutchings, 1997). Clonal fragments perhaps favour endurance strategies and respond to environmental heterogeneity using clonal integration to average conditions over their whole ramet network (Jónsdóttir & Watson, 1997; Oborny & Kun, 2002;

Song *et al.*, 2013). This idea is partially supported by previous work that showed that larger ramets of *R. japonica* (possibly var. *compacta*) translocated resources to support the growth of smaller ramets on the harsh slopes of Mt Fuji in Japan (Suzuki, 1994).

On the other hand, despite an overall lack of statistical significance, clone parts growing in the favourable habitat patches of our heterogeneous treatments appeared to have produced more rhizome branches (per unit of rhizome length), more aerial shoots, and to have accumulated more aerial and rhizomatous biomasses than parts growing in unfavourable patches (Fig. 2b and 2c). Such patterns could indicate the beginning of preferential investments from clones into more favourable habitats. Besides, the shaded patches of the LS treatment harboured part of clones that seemed to exhibit higher specific spacer lengths (Fig. 4), which could be the evidence of a trade-off between phalanx and guerilla growth forms and thus, of a localized escape strategy. Consequently, the absence of clearer morphological and architectural responses is maybe simply linked to the methodological constraints related to the cultivation of giant herbaceous species such as *R. japonica*: i.e. small sample size and short duration of experimentation. A longer experiment and/or a harvest at the end of the growing season would perhaps have given very different results, for instance for the bud bank's distribution (cf. Watson *et al.*, 1997; Gao *et al.*, 2012; Ott & Hartnett, 2015). Further research on this topic would be useful to draw more definitive conclusions.

2.4.2. Establishment potential and management implications

Although this experiment did not aim at investigating the establishment potential of *R. japonica*, it is enlightening to observe that the thirty juveniles survived their first winter and were still growing after 13 month. It is even more interesting when we consider that some of juveniles had to grow under a heavy shade or in a frequently mowed environment. It confirms that three mowing events per year is not sufficient to kill regenerating clones of *R. japonica* (Seiger & Merchant, 1997).

The vegetative propagules that we planted had a fresh weight of approximately 16 g, which represent rhizomes with a length of 12-13 cm for a diameter of 1.2 cm. Such dimensions are certainly not infrequent in the wild where *R. japonica* can annually produce underground biomasses largely exceeding $10 \text{ t} \cdot \text{ha}^{-1}$ (Callaghan *et al.*, 1981; Palmer, 1994). Even our young clones produced largely enough biomass to recreate dozens of such propagules (Fig. 2c). At least two recommendations for the management of *R. japonica* can be made from these observations. First, monitoring campaigns should not overlook shaded habitats as clones born from vegetative propagules may have established there. Second, early control campaigns should either favour the manual extraction of the whole regenerating ramets (e.g. Barthod & Boyer, 2019), or apply much higher frequencies of destruction of the aerial organs to achieve plants' eradication.

Interestingly, clones that experienced only partial mowing (LM treatment) did not produce a significantly lower total biomass than the un-mowed individuals (L treatment). Yet, the contrast with the biomass production of the entirely mowed clones (M treatment) is striking (Fig. 2). It appears thus that the un-mowed halves of the LM treatments managed to

compensate for the loss of their mowed counterparts. This reaffirms the need to mow/cut *R. japonica* individuals over their whole cover to truly impact their growth dynamics (Martin *et al.*, 2019).

Restoration of competitive native species has been shown to be a promising management solution to limit the performances and the spread of *R. japonica* (Skinner *et al.*, 2012; Dommanget *et al.*, 2015; Dommanget *et al.*, 2019). Management by restoration is even more interesting when we consider its environmental impact and cost in the long-term (Dommanget *et al.*, 2019). This kind of restoration using mostly plantings of local species to shade *R. japonica* is frequently associated with mowing during the first years of installation. In this context, it would therefore be very interesting to test the combined effect of shade and mowing on the long-term spatial dynamics of both regenerating and established clones. Besides, it would also be relevant to study the effect of the other aspects of competition (not only for light) on the spatial exploration of knotweed clones.

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– CHAPTER THREE: LOCAL EXPANSION –

As essential as it is to get insights into the growth forms and adaptations of young clonal fragments, the expansion of older individuals in natural conditions possibly differ than that of young clones grown in a mesocosm. Additionally, in many invaded sites, knotweed stands are composed of several aggregated individuals because colonisations often start with the spreading of numerous vegetative propagules (e.g. thanks to floods or to construction works). Because of the closeness of these clonal fragments and the intraspecific competition it leads to, the dynamics of these stands might also be different than what we have seen in the previous chapter. As a consequence, investigating the temporal changes in the cover of established knotweed stands (or patches²) in the wild might be useful to better grasp the effects of various drivers on the vigour and lateral expansion of these plants. For instance, it is an opportunity to assess the long-term effects of regular management operations.

In this new chapter, we will still be interested in the local dynamics of knotweeds, but at a larger spatial and temporal scale than before. Furthermore, as we choose to work in a mountain environment, this work will offer the subsidiary advantage of getting insights on the ability of knotweeds to perform secondary invasions in harsher ecosystems than those of lower elevation.

² In the following article, we use the word « patch » instead of « stand » as it was requested by one of the reviewer during the publishing process. However, we usually prefer the latter word as it avoids confusion with “habitat patches”.



Could knotweeds invade mountains in their introduced range? An analysis of patches dynamics along an elevational gradient

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Abstract

The highly invasive knotweeds (*Reynoutria* spp.) are still infrequent in mountain regions. Despite their current low abundance, they may represent a significant threat for high elevation ecosystems if their population dynamics remain as aggressive as in lowlands during their range expansion to higher elevation. The aim of this study is to assess the knotweed's invasion potential in mountainous regions by studying patch dynamics along an elevational gradient (between 787 and 1666 m a.s.l.) and by reviewing existing literature on their presence and performance in mountains. The outlines of 48 knotweed patches located in the French Alps were measured in 2008 and in 2015 along with biotic, abiotic and management variables. Based on these variables, knotweed's cover changes and patch density were predicted using mixed models. Results showed that elevation has no effect on knotweeds dynamics along the studied elevational gradient. It appeared that the local expansion of knotweed patches is essentially controlled by the patches' initial size and the distance to roads and rivers, i.e. to obstacles and sources of disturbance. Shade and patches' size also impact knotweed patch density, probably through an effect on the species' clonal reproduction and foraging strategies. Interestingly, patches seemed insensitive to the gradient of mowing frequency sampled in this study (between zero and five times per year). All evidences indicate that the knotweed complex is able to colonize and thrive in mountains areas. However, due to the particularities of its spatial dynamics, adequate and timely actions could easily be undertaken to prevent further invasion and associated impacts and reduce management costs.

Keywords *Reynoutria* spp. (*Fallopia* spp.) · Mountain ecosystems · Stand expansion · Diachronic study · Clonality · Invasion process

Introduction

Mountain areas encompass a wide range of ecosystems, host an extremely rich biodiversity and play an important role as refuges for vulnerable species (Huber et al. 2005; Körner 2007). Still, anthropogenic climate and land-use changes strongly modify mountain ecosystems and impact the high biodiversity they host and the services they deliver (Huber et al. 2005). In addition to changing climates and land

abandonment, the introduction and proliferation of invasive alien species also induce severe consequences on native biodiversity and ecosystem processes (Vilà et al. 2011). Long preserved mountains tend now to be increasingly colonized due to growing anthropogenic disturbances (Petryna et al. 2002; Lembrechts et al. 2016) and increased residence time for invasive species (Becker et al. 2005; Alexander et al. 2011), especially in the vicinity of roads (Alexander et al. 2009; Pollnac et al. 2012) which may greatly accelerate their spread (Dainese et al. 2017). Although most exotic and invasive species are still restricted to low- and mid-elevation areas (Becker et al. 2005; Marini et al. 2013), some of them may be found in high-elevation sites and may already represent conservation issues (Becker et al. 2005; Alexander et al. 2009). Therefore, invasive alien species may now be counted as another threat to the conservation of mountain species (Pauchard et al. 2009; Dainese et al. 2017).

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Out of all the potential plant invaders, the complex of species known as knotweeds (*Reynoutria* spp.; syn. *Fallopia* spp., *Polygonaceae*) is of particular concern for conservationists and land managers. The term knotweeds refers to the species *Reynoutria japonica* Houttuyn, *R. sachalinensis* (F. Schmidt) Nakai, hybrids between them (i.e. *R. × bohémica* Chrtek and Chrteková) and any other crosses and backcrosses between these taxa and any other related species (Bailey et al. 2009). Henceforth, the generic term knotweeds will be used when referring to all taxa together and the Latin names will be used to refer to a specific *Reynoutria* taxon. Considered to be among the worst plant invaders in the world (Lowe et al. 2000), knotweeds form dense monoclinal patches (sometimes called “stands”) that are known to have severe impacts on biodiversity, ecosystem processes and anthropic activities: e.g. displacement of native species, alteration of biogeochemical cycles, reduced accessibility to recreational areas, hiding of signalization along roads or railways (Child and Wade 2000; Aguilera et al. 2010; Lavoie 2017). Originated from eastern Asia, knotweeds have successfully colonized most of Europe and North America (Barney 2006; Bailey et al. 2009). In their native range, knotweeds are usually found in ruderal and rather humid habitats, but *R. japonica* is also an early colonist of volcanic deserts, where it plays a very important role for primary successions and has climbed up to 2400 m a.s.l. on Mt Fuji, Japan (Maruta 1983), and 3800 m a.s.l. in the south of Taiwan (Beerling et al. 1994). In the Alps, knotweeds have already been spotted flourishing above 1400 m a.s.l. in Engadin, Switzerland (Beerling et al. 1994) and above 1600 m a.s.l. in various locations of the Belledonne massif, France (Rouifed et al. 2014). Consequently, knotweeds could potentially represent a significant threat to still preserved mountain ecosystems and associated biodiversity.

Without anthropic interventions, knotweeds usually tend to have poor dispersal dynamics at the landscape scale (Tiébré et al. 2008), but once established, knotweed patches are known to be particularly persistent and can therefore serve as sources of propagule for further spread (Pyšek et al. 2003; Barney 2006). Besides, at the local scale, more than presence and dispersal, it is the abundance of invasive species’ stems and their cover dynamics that determine their impact on biodiversity (Pauchard and Shea 2006; Kettenring et al. 2016). For clonal species like knotweeds, potential impacts would, therefore, be related to a great extent to clonal patches’ characteristics such as size, lateral expansion rates and ramet density (Barney et al. 2006; Gerber et al. 2008; Kettenring et al. 2016) since knotweed form dense monoclinal patches that outcompete and exclude other plant species.

However, little is known about what drives knotweed patches’ dynamics. Some authors argue that biotic and abiotic variables do not explain the size of knotweed patches (Palmer 1994; Bímová et al. 2004; Dommanget 2014) and

that they are only a function of their age (Adachi et al. 1996a, b; Bímová et al. 2004). On the contrary, others stated that mowing could promote dispersal risks (Child and Wade 2000; McHugh 2006) and the lateral expansion of knotweed patches (Beerling and Palmer 1994; Seiger and Merchant 1997). Mowing is also likely to promote patch densification (Child and Wade 2000; Gerber et al. 2008; Urgenson et al. 2009). The density and performances of knotweed patches are additionally known to be rather sensitive to light reduction, even to slight shading (Seiger 1993; Beerling et al. 1994; Dommanget et al. 2013). Nevertheless, they are still capable of invading various forest ecosystems (Dommanget et al. 2016) and the effects of shade on the spatial dynamics of these plants remain poorly understood, particularly in interaction with mechanical control.

The aim of the present study was to assess the likelihood of the knotweed complex to thrive in mountain ecosystems by highlighting the relative effect of elevation, mowing, shade, and their interactions, on the local dynamics of knotweed patches. For this purpose, a diachronic survey of knotweed patches was conducted along an elevational gradient in the French Alps in order to explore which biotic, abiotic and management factors best explain the cover changes and the ramet density of knotweed patches.

Despite the strong interest of revisiting approaches to characterize patches’ dynamics, this approach is seldom used in invasion ecology studies (but see Kettenring et al. 2016) and was never undertaken at the patch scale for the knotweed complex. As some authors have emphasize the need to investigate the pre-adaptation of invasive alien species to mountain environmental conditions (Marini et al. 2013), this empirically based approach is also put in the context of the current literature on the performance and dynamics of knotweeds in mountainous regions to better evaluate the risk of mountain invasion and discuss implications for management and conservation of mountain ecosystems.

Materials and methods

Study area and sampling design

The study area was located across four mountain ranges (Belledonne, Chartreuse, Trièves-Matheysine, and Vercors) of the French Northern Alps (Fig. 1). The Chartreuse and Vercors ranges are part of the French Prealps and are characterized by a limestone substratum and a mountain climate with oceanic influences. The Belledonne mountain range is a crystalline massif of the outer Alps with a mountain climate. The region called “Trièves-Matheysine” is a mixed plateau and hilly area between the Prealps and the outer Alps (Taillefer massif) characterized by a mountain climate with Mediterranean influences. Human population

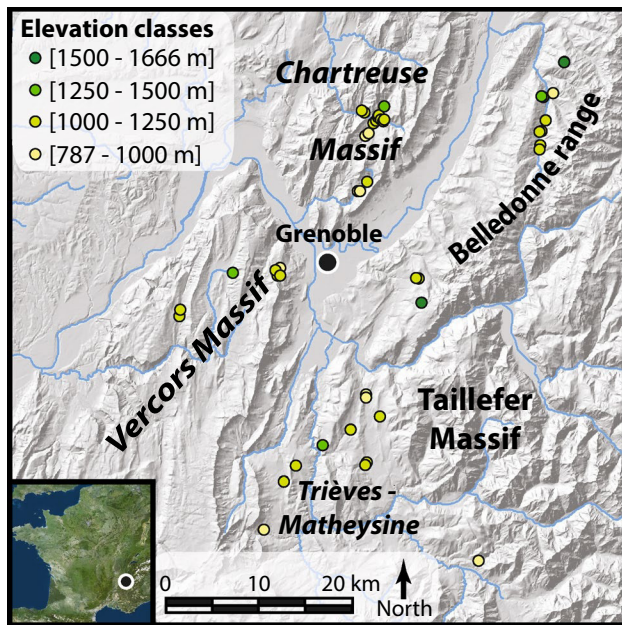


Fig. 1 Study area in the French Alps. The location of the knotweed patches studied is indicated by the dots. Main rivers are indicated by lines. (Figure made with Adobe Illustrator)

is low in these areas, but the presence of agricultural, forestry and tourist activities induces regular anthropogenic disturbances.

A total of 48 patches varying from less than 1 m² to more than 350 m² were selected. Patches were quite equally distributed among the four mountain ranges and occurred along an elevational gradient ranging from 787 m to 1666 m a.s.l. They experienced different environmental conditions and occurred on varied land-use types (i.e. in decreasing order of importance: road and trail verges, forest edges, wastelands, fields, river and stream banks, and house gardens).

The outline of each knotweed patch was first measured in 2008 (Rouified et al. 2014). In 2015, all patches were revisited and mapped again using high-accuracy GPS (Trimble Geoexplorer 6000 with theoretical horizontal accuracy of 50 cm). If new patches were detected growing less than 2 m away from the patch measured in 2008, they were mapped as being part of the studied patch, if further away, patches were disregarded as their origin could be unrelated to the studied population and come from external sources (e.g. from dumping of green wastes, or transport of soil contaminated with plant fragments during construction works). Indeed, this study focused on patch expansion dynamics only and not colonization processes. This two-metre limit was chosen because our field observations indicated that rhizomes rarely extended further than 2 m away than patches' edges. These observations have since been empirically confirmed (Fennell et al. 2018).

Patch characterization

For each patch, the *relative* (%—"PercentEvo") and the *absolute* cover change (m²—"AbsolEvo") between 2008 and 2015 were computed based on the GPS measurements. The number of stem per m² ("Ramet density") was measured using one randomly placed 1-m² quadrat within small patches (< 10 m²), and averaged based on two quadrat measurements for medium patches (between 10 and 20 m²) and three quadrat measurements for large patches (> 30 m²).

At the edge of each patch, four sampling points were placed in the four cardinal directions. At each sampling point, the percentage cover of graminoids and forbs in front of the patch were visually estimated on a 1 m² square plot, the percentage cover of shrubs on a 25 m² square plot and the percentage cover of trees on a 100-m² square plot to investigate if these various growth types could affect the dynamics of knotweed patches. These cover estimates were then compiled and averaged to get a single cover value per vegetation type for each patch. To characterize soil properties, one soil core was extracted using a drilling auger (Ø 7 cm, depth 20 cm) in each sampling point centre, pooled together per patch and analysed in the laboratory in order to estimate five granulometric classes as well as pH and C:N ratio following procedures of the French Standardization Association (i.e. AFNOR).

Environmental variables

To explain variations in the patches dynamics of knotweeds, three groups of explanatory variables were used (Table 1). Biotic variables were the 2008 patch area ("PatchArea"), used to assess the effect of patches' initial size on knotweed dynamics, and the total cover percentages of shrub and tree ("Shade"). Abiotic variables were the distance to the nearest road or river ("DistanceLLF"; i.e. LLF linear landscape feature), the mean slope ("Slope") measured with a clinometer, the mean elevation ("Elevation") measured with the GPS, and a synthetic soil granulometry and fertility variable ("Soil") which was extracted from the first axis of a normed-PCA (Principal Component Analysis) performed on all soil variables and that separated patches growing on rich sandy soils from unfertile rocky soils (see Online Resource 1). Management variables were mowing frequency at each patch (i.e. mean number of mowing events per year since 2008; "MowFreq") and a binary variable indicating if patches were entirely mowed or not ("Fullmow").

Data analysis

Analyses were performed with R version 3.3.2 (R Development Core Team 2016). Based on data exploration (Zuur et al. 2010), explanatory variables with a skewness > 1 were

Table 1 Presentation of the response and explanatory variables retained for analysis

Variable name	Definition	Unit
Response variables		
RelatEvo	Relative cover change between 2008 and 2015	%
AbsolEvo	Absolute cover change between 2008 and 2015	Sq. metres
Ramet density	Mean ramet density	Number per sq. metres
Explanatory variables		
Biotic variables		
PatchArea	Patch area in 2008	sq. meters
Shade	Addition of the shrub and tree cover percentages	%
Abiotic variables		
DistanceLLF	Distance to the closest linear landscape feature (i.e. road or river)	m
Slope	Angle of the main slope	°
Elevation	Mean elevation	m a.s.l
Soil	Synthetic soil granulometry and fertility variable (i.e. a gradient between rich-fine soils and poor-coarse soils)	PCA axis coordinates
Management variables		
MowFreq	Frequency of management by mowing	Times per year
Fullmow	Binary variable showing if patches are entirely mowed or not	–

A bivariate plot of the three response variables plotted against every explanatory variables is available in Online Resource 2

log or log + 1 transformed to approximate normal distribution, and predictors with Variance Inflation Factors (VIF) > 2 were excluded to avoid collinearity issues.

The effect of explanatory variables (or interaction between them) on knotweed patches dynamics was tested using linear models. Because knotweed patches were not spatially independent and as spatial autocorrelation in observation studies often leads to biased standard error estimates, we used mixed models in which “site” was included as random effect. A “site” was defined as a group of knotweed patches clustered in an area with a maximum radius of 2.5 km and characterized by relatively similar abiotic conditions. A total of 44 biologically plausible a priori candidate models (plus a null model) were built for each response variable: i.e. patches relative and absolute cover change and ramet density (for a complete list of all candidate models, see Online Resource 3 and 4). Model selection was then applied to find the most parsimonious models. This approach was chosen because it enabled hypotheses testing on the focal predictors (i.e. elevation, shade and the mowing variables) while controlling for the potential effects of other covariates (i.e. patch area, distance to an LLF, soil and slope).

Since all response variables were over-dispersed, negative binomial GLMMs (Generalized Linear Mixed Models) were used (Warton et al. 2016). Response variables (Y) were first to be rounded up and made positive (Y') by adding a constant (C) with $C = 1 - \min(Y)$ resulting in $\min(Y') = 1$. Mixed models were then fitted using Laplace approximation (Bolker et al. 2009). To identify the most parsimonious regression models, Akaike’s Information Criterion corrected

for small sample sizes (AICc) was used, with top-ranked models being those for which the delta of AICc was < 2 (Burnham and Anderson 2002). However, due to the interaction terms used in some models, model averaging was not recommended (Cade 2015). Therefore, all top-ranked models were interpreted as they were (Bolker et al. 2009). To provide an estimate of the goodness of fit of our models, the marginal coefficient of determination for fixed effect parameters alone (R^2_{GLMM}) was computed for each model (following Nakagawa et al. 2017).

Results

Patches evolution between 2008 and 2015

Knotweed patches in the study area spread substantially between 2008 and 2015 (Table 2). Their average absolute

Table 2 Descriptive statistics for knotweed patches’ dynamics in a mountainous region of the French Alps

	Mean (\pm SD)	Median	Min	Max
Response variables				
RelatEvo (%)	59.15 (\pm 66.66)	34.46	– 9.75	251.10
AbsolEvo (m ²)	18.46 (\pm 21.11)	10.55	– 5.61	70.62
Ramet density (nb. per m ²)	22.06 (\pm 12.36)	20.00	6.00	53.50

For details on variables and their names, see Table 1

cover change was about +20 m², which represented a mean increase of about 60%, although with high variability. Interestingly, although seven patches gained more than 50 m² in 7 years, seven apparently lost ground.

Drivers of knotweed relative and absolute cover changes

In the study area, changes in both the relative (i.e. “RelatEvo”) and the absolute cover (i.e. “AbsolEvo”) were best predicted by model 24 (see Online Resource 3) which accounted for the patch area in 2008 and the distance to an LLF. Although this top-ranked model explained around 25% of the variation in knotweed cover changes (Table 3a and 3b), results showed that other models also received a certain level of support (i.e. delta AICc < 2). Consequently, the three top-ranked models for the relative cover change and the five top-ranked models for the absolute cover change were interpreted.

For the relative cover change, the patch area had a significant negative effect in all top-ranked models while the distance to an LLF had a significant positive effect in the only selected model in which it occurred as a predictor (Fig. 2a). The fully mowed patch variable had a non-significant negative effect in the third and last top-ranked model and its contribution to the R^2_{GLMM} was weak; i.e. R^2_{GLMM} with and without this predictor are relatively similar (Table 3a).

For the absolute cover changes, the patch area had a significant positive effect in the five selected models in which it occurred, as did the distance to an LLF in the two top-ranked models where it was present as a predictor (Fig. 2b). Both elevation and the fully mowed patch variable only occurred

in one top-ranked model and had a non-significant negative effect on knotweed absolute cover changes. Conversely, shade had a non-significant positive effect on this response variable (Fig. 2b).

Drivers of knotweed patches’ ramet density

Ramet density was best predicted by model 30 (see Online Resource 4) which accounted for patch area and shade (Table 3c and Fig. 2c). Both predictors had highly significant effects, positive for the patch area and negative for shade (Fig. 2c) and explained almost 43% of the variance of the response variable (Table 3c).

It is also worth noting that, since 2008, a total of 18 new patches of knotweed have been found in the vicinity (< 150 m) of the study sites.

Discussion

Overall, the results showed that knotweed patches are expanding locally and that this dynamic was not mediated by the elevational gradient and mowing operations. Actually, the most important factors controlling the cover changes of knotweed patches are the original patch area (i.e. in 2008) and the distance to an LLF, i.e. a road or a river, while ramet density is mostly influenced by shade and the patch area.

Driving factors of knotweed patches dynamics

Results globally acknowledge the importance of the initial patch area and the distance to an LLF to explain the changes

Table 3 Top-ranking (i.e. delta AICc < 2) models among 45 GLMMs predicting relative (a) and absolute changes (b) of knotweed patch covers, and ramet density (c) as assessed by Akaike’s Information Criterion corrected for small samples (AICc)

Fixed effect(s)		<i>k</i>	AICc	<i>W</i>	R^2_{GLMM}
(a) Top-ranked models for ‘RelatEvo’					
Log(PatchArea)	+	3	497.20	0.324	0.257
Log(PatchArea)		2	498.17	0.199	0.205
Log(PatchArea)	+	3	499.01	0.131	0.226
(b) Top-ranked models for AbsolEvo					
Fixed effect(s)		<i>k</i>	AICc	<i>W</i>	R^2_{GLMM}
Log(PatchArea)	+	3	403.13	0.211	0.233
Log(PatchArea)		2	403.75	0.155	0.141
Log(PatchArea)	+	3	404.14	0.128	0.163
Log(PatchArea)	+	4	404.85	0.089	0.248
Log(PatchArea)	+	3	404.92	0.086	0.162
(c) Top-ranked model for ‘Ramet density’					
Fixed effect(s)		<i>k</i>	AICc	<i>W</i>	R^2_{GLMM}
Log(PatchArea)	+	3	345.87	0.678	0.428

Models are ranked based on their AICc values, and the number of estimated parameters including the intercept (*k*), AICc, AICc weight (*W*), marginal coefficient of determination for fixed effect (R^2_{GLMM}) are provided. For details on variables description, see Table 1

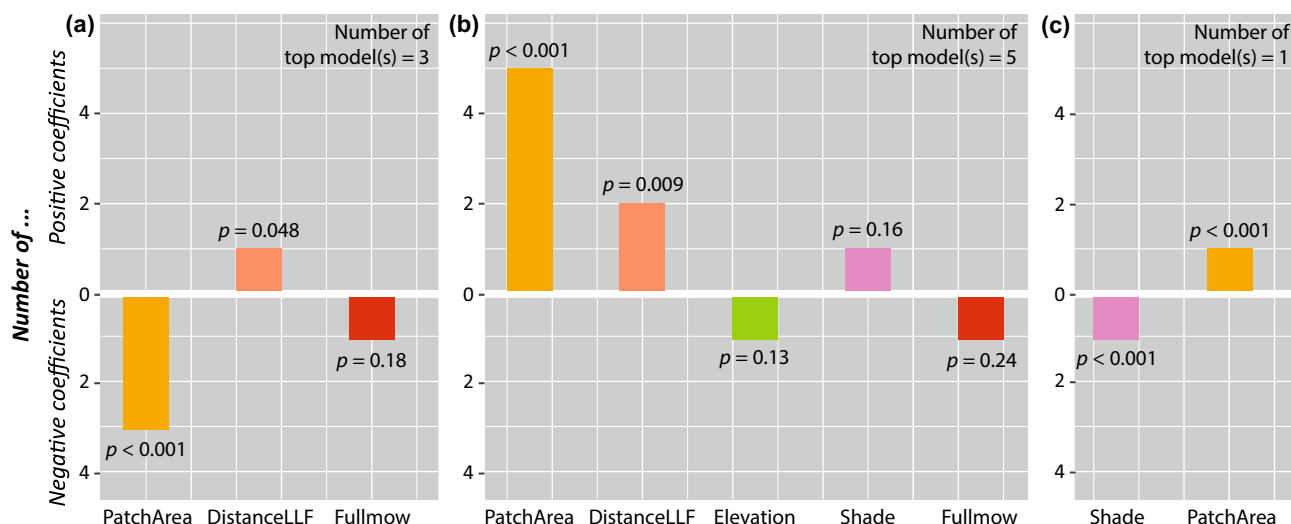


Fig. 2 Summary of the positive and negative effects of each predictor in all the top-ranked models in which they occur to predict relative (a) and absolute changes (b) of knotweed patch covers, and their ramet density (c) as assessed by Akaike's Information Criterion cor-

rected for small samples (AICc). The lowest p value for each predictor is displayed. Predictors are ranked based on their p values. For details on variables, see Table 1

of cover of knotweed patches. Consistent with other studies (Beerling and Palmer 1994), a negative effect of patch area on the relative cover change and a positive effect on the absolute expansion was observed. This means that a large patch, with potentially lots of reserves in its rhizomes, may easily increase its area (m^2) but that this expansion is relatively small compared to its original size (%). This pattern suggests that small patches may have higher lateral growth rates than large patches. Higher relative growth rate for young patches may be a way to ensure spatial pre-emption in order to avoid competitive exclusion by other plant species (Herben and Hara 1997; Suzuki and Hutchings 1997). Some authors stated that knotweed patches grow centrifugally with time, implying that patch expansion is only controlled by age and therefore size (Adachi et al. 1996a, b; Bímová et al. 2004; Smith et al. 2007; Dommanget 2014). While it is likely that knotweed patches tend to expand with time, the relation between age and rate of lateral expansion may not be linear for the entire life of the patch. Additionally, patch area may be a poor proxy for the age of knotweed patches and could, thus, bias observations on expansion dynamics. Given that fragment spread is one of the major dispersal means of knotweeds in their introduced range (Beerling et al. 1994; Barney et al. 2006), the “individuality” of patches cannot be ascertained and many large patches can purely result from the initial spreading of many rhizome and/or stem fragments. Large patches may consequently expand more because of strong intraspecific competition between several “individuals” that are forced to expand directionally as they cannot exclude each other (de Kroon et al. 1992).

On the other hand, Pyšek et al. (2003) also stipulated that the size of a patch was determined by the ability of its genotype to produce early shoots and that local disturbances could also impact the expansion of a patch. This is consistent with the present study that shows that other variables are to be accounted for to explain knotweeds' spatial dynamics at the patch scale, especially the distance to an LLF. The positive influence of the distance to a road or a river on knotweed expansion is likely explained by the obstacle effect of such LLF and by the disturbances it creates (e.g. raking, stamping and crushing, pollution by road salt or hydrocarbon, floods), occasionally depleting reserves or altering the performances of the plant, which would impede future growth. Consequently, although the proximity of dispersal vectors such as roads or rivers favours the regional dispersal dynamics of knotweeds (Pyšek et al. 2003; Duquette et al. 2015), it appears to be an impediment for expansion at the patch scale. This reinforces the idea that a focus on multiple spatial scales is needed when one tries to examine possible causal factors on invasion processes (Pauchard and Shea 2006).

In our study design, a choice was made to disregard new patches (i.e. present in 2015 but not in 2008) more than 2 m away from the focal patch because certainty as to their origin could not be ensured. Yet knotweeds are known to produce running rhizomes up to several metres away from the main patches (Child and Wade 2000), which could likely sprout into new ramets. On the contrary, such ramets could have been created by the dispersal of fragments due to careless mowing, floods or other disturbances. These problems, inherent to the study of the spatial dynamics of clonal plants

and very hard to take into account, may hide strong and significant drivers and processes.

Beyond their cover, the impact of knotweed patches on native species and ecosystem functions is linked to a large extent to their density (Urgenson et al. 2009; Lavoie 2017). In the study area, shade significantly reduced the number of stems per square metre (Fig. 2c). This could be the result of two non-mutually exclusive processes. When shaded, knotweed could simply be too weak to produce a great number of stems. Alternatively, this could likely be a clonal foraging strategy. In heterogeneous habitats, as a result of their wide perception of their environment, some clonal plants are able to selectively place their ramets in favourable patches, such as luminous ones (Slade and Hutchings 1987), hence enhancing the overall fitness of the plant (Hutchings and de Kroon 1994; de Kroon et al. 2009). Consequently, in luminous patches, it would be advantageous for knotweeds to produce more stems and, thus, to have a high ramet density to maximize light interception while being density controlled by physiological integration to avoid excessive intra-plant competition (Suzuki and Hutchings 1997). This strategy is called a phalanx growth form (Herben and Hara 1997). In contrast, under the canopy of trees and shrubs, it would be more advantageous to produce fewer stems, either to avoid any inter-ramet competition for the scarce light resource or to actively search for luminous patches, i.e. a guerrilla growth form (Herben and Hara 1997). Clonal plants can even operate trade-offs between these two growth forms (Ye et al. 2006). Hints of such responses have already been observed for knotweeds (Dommanget 2014). In this context, the positive effect of patch area on ramet density (Fig. 2c) could be due to an optimal ramet density that is size- or age-dependent (Suzuki 1994; Adachi et al. 1996b). Since most of the patches in the study area were fairly small, they would not yet have reached the optimal density.

Interestingly, mowing frequency (even in interaction with the fully-mowed patch variable) does not seem to affect the expansion dynamics or the ramet density of knotweed patches. Mowing frequency sampled in this study ranged from zero to five times per year, which is probably insufficient to truly impact knotweed dynamics as has been shown in other studies (Seiger and Merchant 1997; Gerber et al. 2010).

Assessment of the invasion risk of knotweeds in mountain areas

The fact that elevation shows no clear influence on knotweed patches' dynamics along our altitudinal gradient is not utterly surprising. In their native range, knotweeds can be found from sea level to mountain tops, the actual upper distributional limit being highly dependent on latitude. Even though studies are lacking for the other taxa, at least *R.*

japonica is well adapted to high-elevation environments in its native range, as shown by the literature on its physiology and adaptation to elevation (for a review, see: Barney et al. 2006). If the exact sampling locations of the *R. japonica* and *R. sachalinensis* genotypes introduced in Europe cannot be found with absolute certainty, their most probable regions of origin are the coastal-mountainous regions of Honshu and Hokkaido in Japan (Pashley 2003; Pashley et al. 2007). It is then plausible that introduced knotweeds may already be pre-adapted to high-elevation environments. Moreover, the high hybridization potential of knotweeds likely increases the invasiveness of the hybrids (Bailey et al. 2007; Krebs et al. 2010; Parepa et al. 2014), probably also in mountain areas. Both aspects as well as broad environmental tolerance are important to determine the capacity of a species to invade mountain environments (Alexander et al. 2009, 2011; Pauchard et al. 2009), especially in a changing climate as has been shown for other invasive alien species (Moran et al. 2017).

Many studies and observations support the assumption that knotweeds are well adapted to harsh abiotic environments. As previously mentioned, thriving patches of all three knotweed taxa were found quite high on various locations of the Alps (Beerling et al. 1994; Rouifed et al. 2014), as well as in the Gaspé Peninsula in Quebec (48°28'N) (Groeneveld et al. 2014) and far beyond the Arctic Circle in Norway, north of Tromsø (69°39'N) (Holm et al. 2017). In general, it is assumed that the distribution of *R. japonica* (that of *R. sachalinensis* being probably slightly more restrained) is found in regions with a sum ≥ 2505 day-degrees and an absolute minimum temperature ≥ -30.2 °C (Beerling 1993; Bouchier and Van Hezewijk 2010). Such a wide climatic range could likely encompass many mountain regions of knotweeds' introduced range provided that precipitation is sufficient, as knotweeds do not grow in regions with precipitations below 500 mm/year (Beerling et al. 1995). A small test experiment in the Grande Rousse massif (France) showed that rhizome fragments of the hybrid *R. × bohemica* can regenerate and grow for at least 2 years in grasslands and screes of the montane (ca. 1100 m a.s.l.) and subalpine (ca. 1950 m a.s.l.) vegetation belts, as well as in alpine grasslands around 2550 m a.s.l. (Spiegelberger et al., unpublished). Marigo and Pautou (1998) also reported that in the Alpine Garden of Lautaret (French Alps, ca. 2200 m a.s.l.), *R. sachalinensis* patches were able to regenerate new shoots even after two harsh winters where temperatures dropped to around -20 °C. In Japan, Maruta (1983) showed that there were no differences in relative growth rates between low- and high-elevation *R. japonica* seedlings and that winter survival was possible at high elevations as long as a minimum dry-matter production was achieved during the growing season. Shimoda and Yamasaki (2016) furthermore stated that there was no clear relationship between stem height and

elevation in a survey of 33 *R. japonica* populations located from the sea level to their upper distributional limit (i.e. 2415 m a.s.l.).

Along the same elevational gradient and sites as the present study, the probability of the presence of knotweeds has been shown to be unrelated to elevation (Rouified et al. 2014). In the same region, but on a smaller elevational gradient, Dommanget (2014) additionally found that the performances of knotweed patches could not be explained by elevation. The present results (Table 3; Fig. 2) show that patches' expansion and ramet density are not directly controlled by elevation either. All these evidences suggest that knotweeds have not yet reached the limits of their climatic niche in the French Alps and may be perfectly able to colonize and thrive at high-elevation sites. If propagules are brought to such locations, which is likely in the light of the growing human pressure on mountain environments (Huber et al. 2005; Dainese et al. 2017), they may cause significant impacts on valuable mountain ecosystems. To date, the only study suggesting an alternative conclusion reports that elevation increased the population turnover rates of *R. japonica* (among many other invasive alien species) in the Swiss Alps (Seipel et al. 2016). Their conclusion is based on the fact that some *R. japonica*'s "populations" went extinct between 2003 and 2009 presumably by the sole effect of harsh climatic conditions. However, if this may be plausible for seedlings [such seedlings would yet likely belong to *R. × bohemica* and not *R. japonica* since, in Western Europe, the latter has (to the best of our knowledge) always been found to be represented by a single male-sterile clone (Bailey et al. 2009; Buhk and Thielsch 2015)], this would be highly surprising for established patches born from plant fragments as natural mortality is considered to be incredibly rare for this clonal perennial species. Consequently, it is reasonable to think that other factors than elevation may have affected the turnover rates of *R. japonica*'s populations.

An insidious invader that requires cautious management

Without human dispersal, invasion rates of knotweeds towards higher elevations should be slow as the mode of reproduction of knotweeds in their introduced range is primarily vegetative (Bailey 1994; Beerling et al. 1994). Seedlings are indeed quite rare for at least two reasons: firstly, being mostly of hybrid origin (except for *R. sachalinensis*), they depend on the presence of the right "constellation of parental populations" (Funkenberg et al. 2012). Secondly, knotweed seedlings are very sensible to climatic conditions, have a slow growth rate, and lack competitive abilities (Bailey 2003; Funkenberg et al. 2012). As they are highly sensible to late frost (Maruta 1983; Funkenberg et al. 2012), they may be even rarer in mountains than in lowlands. However,

if sporadic knotweeds do establish and gather reserves, whatever their origin, they will be extremely time consuming and expensive to remove. Although their presence does not necessarily mean immediate heavy impacts, these perennial clonal plants could represent a threat in the long-term (i.e. an "impact debt"). Even small, patches could endure until a disturbance enables them to spread and further increase propagule pressure in the area. For instance, a riverine patch could gradually colonize downstream banks with every flood (e.g. Duquette et al. 2015), or clearcuttings of invaded forest stands could enable knotweeds to dominate and prevent tree regeneration, as is feared by many forest managers (Dommanget et al. 2016). Land managers and decision makers in the elevated regions of Europe and North America should therefore act accordingly.

To prevent such a creeping invasion process, timely actions should be carried out. First of all, transportation of stem or rhizome fragments (e.g. in contaminated earth, in green wastes, in construction or mowing machinery) should be avoided. Extensive monitoring should also be conducted to detect any new establishment of knotweed and, if needed, to apply early control measures on these new populations such as uprooting or intensive mowing. During the course of this study, 18 new knotweed patches have indeed been found less than 150 m away than the studied patches (more patches probably exist between our study sites), indicating that new colonizations are happening, whatever their origin. Despite the rarity of sexual reproduction in knotweeds, management of established patches before flowering could also be useful to ensure the absence of any seed dispersal event. Finally, all these efforts should be maintained over time and conducted at a regional scale through an effective coordination of the various stakeholders.

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Author contributions FMM, FD, TS and AE designed the present study; FMM, FD, PJ, CV and TS collected the data; FMM, PJ and CV analyzed the data; FMM wrote the original manuscript, and all authors contributed substantially to the manuscript improvement and validation.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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– CHAPTER FOUR: LARGE SCALE DATA ACQUISITION –

At the landscape scale (or higher scales), the study of the dynamics of any plant invader gets confronted with the perpetual problem of data acquisition. Being able to infer simple understanding or broad generalisations on spatiotemporal processes implies to have access to information on the variation of patterns in space and time. At large spatial scale, gathering such data is often highly time- and money-consuming, limiting our abilities to progress towards high fidelity predictions.

Getting access to large scale data is also of prime importance for many managers as it is one of the keys to assess the invasion status of an area, prioritize control efforts, assess the long-term effects of management, or undertake early control actions when the data highlight newly arrived populations.

In this methodological chapter, we will offer a contribution to the resolution of this recurring issue by proposing a method to acquire high accuracy data on knotweeds cover at different scales by performing classifications on satellite and UAV imagery (*unmanned aerial vehicle*).

Article

Using Single- and Multi-Date UAV and Satellite Imagery to Accurately Monitor Invasive Knotweed Species

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Abstract: Understanding the spatial dynamics of invasive alien plants is a growing concern for many scientists and land managers hoping to effectively tackle invasions or mitigate their impacts. Consequently, there is an urgent need for the development of efficient tools for large scale mapping of invasive plant populations and the monitoring of colonization fronts. Remote sensing using very high resolution satellite and Unmanned Aerial Vehicle (UAV) imagery is increasingly considered for such purposes. Here, we assessed the potential of several single- and multi-date indices derived from satellite and UAV imagery (i.e., UAV-generated Canopy Height Models—CHMs; and Bi-Temporal Band Ratios—BTBRs) for the detection and mapping of the highly problematic Asian knotweeds (*Fallopia japonica*; *Fallopia* × *bohemica*) in two different landscapes (i.e., open vs. highly heterogeneous areas). The idea was to develop a simple classification procedure using the Random Forest classifier in eCognition, usable in various contexts and requiring little training to be used by non-experts. We also rationalized errors of omission by applying simple “buffer” boundaries around knotweed predictions to know if heterogeneity across multi-date images could lead to unfairly harsh accuracy assessment and, therefore, ill-advised decisions. Although our “crisp” satellite results were rather average, our UAV classifications achieved high detection accuracies. Multi-date spectral indices and CHMs consistently improved classification results of both datasets. To the best of our knowledge, it was the first time that UAV-generated CHMs were used to map invasive plants and their use substantially facilitated knotweed detection in heterogeneous vegetation contexts. Additionally, the “buffer” boundary results showed detection rates often exceeding 90–95% for both satellite and UAV images, suggesting that classical accuracy assessments were overly conservative. Considering these results, it seems that knotweed can be satisfactorily mapped and monitored via remote sensing with moderate time and money investment but that the choice of the most appropriate method will depend on the landscape context and the spatial scale of the invaded area.

Keywords: *Fallopia* spp. (*Reynoutria* spp.); invasive plant management; applied remote sensing; spatial dynamics monitoring; Unmanned Aerial Vehicle (UAV); very high resolution satellite imagery

1. Introduction

Biological invasions are usually seen as a major cause of global change that threatens biodiversity, ecosystem functioning, economies and human well-being [1]. As early monitoring and management of invasive alien plants (IAPs) is recognized as one of the most cost-efficient ways to tackle invasions [2],

the elaboration of operational methods to quickly detect IAPs over large areas is particularly needed [3]. Consequently, an increasing number of studies have been published on the identification and mapping of IAPs using remote sensing technologies (for reviews, see: References [4,5]). Remote identification of plants was historically limited to trees and shrubs, but the rise of very high resolution (VHR) satellites and of Unmanned Aerial Vehicles (UAVs) with sub-metric to sub-decimeter spatial resolutions has led the way to the accurate mapping of herbaceous invaders [6]. VHR satellites have the advantage to cover large spaces of land on a regular basis while UAVs offer unmatched spatial and temporal resolutions for reasonable prices [7,8].

Japanese knotweed (*Fallopia japonica*; syn. *Reynoutria japonica*, *Polygonum cuspidatum*) and Bohemian knotweed (*Fallopia × bohemica*; syn. *Reynoutria × bohemica*, *Polygonum × bohemicum*) are among the most troublesome IAPs for land managers and conservationists in temperate regions of the world. Originally from eastern Asia, they have colonized countless areas of Europe, North America, Australia and New Zealand [9,10]. These highly competitive, fast-growing herbaceous plants are characterized by a wide environmental tolerance, strong regeneration capacities, important hybridization potential and both clonal and sexual reproduction [11,12]. Consequently, knotweeds are known to be extremely difficult to control, and their management has been the focus of numerous publications and reviews (e.g., References [13–15]). The annual economic cost of knotweed invasions is estimated to be around €2.3 billion in Europe [16] and above £165 million for the United Kingdom alone [17].

Improving detection and monitoring of knotweed populations could enhance control efficiency and decision making (c.f. [2,18,19]) and lead to a better understanding of their spatial dynamics [19,20], especially along their main dispersal axes—i.e., transportation corridors and rivers [21].

Unlike many woody species, the remote detection of herbaceous IAPs can be quite challenging as it usually requires very high spatial resolutions and implies that plants should have aggregated populations and not scattered growth habits [22–24]. Still, many studies report successful mapping of invasive herbaceous species using either hyperspectral sensors (e.g., References [25,26]), VHR satellite imagery (e.g., References [27–29]) or UAV imagery (e.g., References [30–32]). The number of possible approaches is quickly growing, but the detection remains highly species-specific [5,23]. Until recently, attempts to remotely detect knotweeds remained inconclusive (e.g., [33,34]). Müllerová et al. [35], however, used the extremely high spatiotemporal resolution of low-cost UAV imagery to track the phenological stages of the plant and finally reached classification accuracies suitable for operational applications with an image acquired in November, when the senescent plant differed most from the surrounding vegetation. However, since others failed to map knotweed with comparable images due to bad illumination and long projected shadows [36], and as this method is highly dependent on weather conditions and the duration of the senescence stage, alternative methods were needed.

An effective way to improve image classification results for a plant species that lacks a distinctive phenological response (e.g., distinct flowering organs) is to increase the number of variables used to describe this elusive response (e.g., spectral channels, texture features). Indeed, more variables mean more chances to uniquely specify the characteristic response of the plant. Hyperspectral images, with their many spectral bands, are commonly used for such a purpose [22]. For a long time, hyperspectral images had relatively coarse spatial resolutions [22,27]. The development of UAV-embedded hyperspectral sensors now offers very high spatial resolution, but these data are often difficult to handle for non-experts and would therefore be impractical for operational uses at the moment (c.f. [35]). Alternatively, the use of multi-date imagery to assess spectral differences in time has given promising results for IAPs detection [28,37], although it was unfruitfully tested for knotweeds [33]. The progress in the photogrammetry of UAV images also enables easy generation of 3D models that highlight the structure of vegetation [38,39], which may be helpful to distinguish plant growth forms.

In this applied study, our aim was to: (i) assess the potential of single- and multi-date variables for the success of knotweed detection from satellite and UAV imagery, (ii) evaluate the percentage cover of knotweed detected from both remote sensing platforms, and (iii) describe an easily reproducible

classification procedure for the accurate mapping of knotweeds. Since remote sensing techniques are often too complex to be implemented by non-experts, we aimed to reduce the complexity by using commercial software that requires little training and data that are relatively easy to acquire and process. Our proposed methodology thus has the potential to become operational in practical management and ecological conservation.

2. Materials and Methods

2.1. Study Sites and Image Acquisition

In this study, we worked on two different sites located in the floodplains of two major rivers of eastern France (Figure 1). For each site, a set of satellite and UAV images were acquired at three different time periods: spring, early summer and early fall (Table 1). Unfortunately, a crash of our UAV prevented us from acquiring the summer UAV images (the UAV was repaired in time for the early fall flights).

The satellite imagery consisted of Pleiades 1B PMS images with a 50 cm spatial resolution (the 2 m multispectral bands were pan-sharpened using the 50 cm panchromatic Pleiades bands), and a four-channel (RGB + NIR) spectral resolution.

The UAV images were obtained via a DS6 hexacopter UAV [DRONESYS, Saint Vincent de Mercuze, France]. The DS6 had a diameter of 80 cm for an approximate weight of 8 kg and could carry a payload of 3.5 kg. The UAV was equipped with two commercial cameras (Sony Alpha 7 with 24.3 Megapixels Full Frame Exmor CMOS Sensor and a Sonnar T* FE 35mm f/2.8 Zeiss lens). One camera was used to catch standard RGB bands while the other had been modified to acquire the near-infrared part of the spectrum (NIR): i.e., the built-in filter was replaced by MC Clear and Hoya R72 filters. The two cameras were embedded in a three-axis actively stabilized gimbal that controls for pitch and roll through the use of motors linked to AHRS sensors. The navigation and on-flight stability of the aircraft was managed by an A2 flight control system [DJI, Shenzhen, China]. Flight missions were pre-programmed and performed by the auto-pilot under the supervision of two pilots and a ground-control station. This low-cost flexible platform enabled the acquisition of 8 cm resolution imagery.

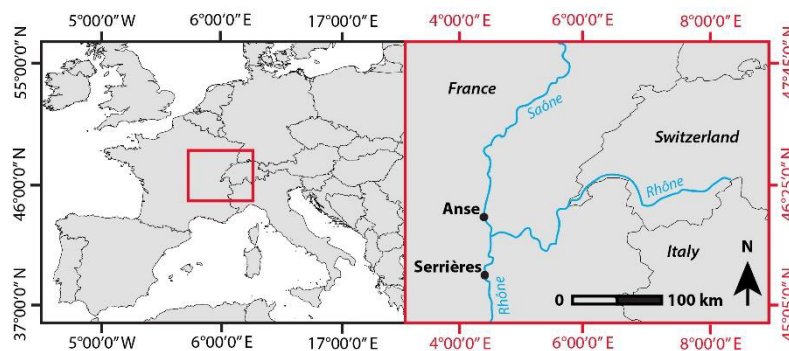


Figure 1. Locations of the study sites.

The Anse site (ca. 170 m a.s.l.) was located at the confluence of the Saône River and one of its tributaries, the Azergues River, whose banks are heavily invaded by knotweeds. The Anse Pleiades images covered an area of 213 ha comprising urban areas, croplands, major transportation infrastructure and semi-natural riparian environments. The UAV study area represented a 4.8 ha subset of the area covered by the Pleiades image and was characterized by highly heterogeneous riparian vegetation at the junction of the rivers. Some knotweed stands in the area are frequently mowed while others are unmanaged. The Serrières site (ca. 132 m a.s.l.) was located along the Rhône River. The Pleiades imagery covered an area of 263 ha composed of urban areas, various agricultural lands (vineyards, orchards and crops), forests and mostly-open riverbanks (recreational area) sporadically invaded by knotweeds. The UAV site covered an area of 7.1 ha and was restricted to an open riverbank

zone of the site that hosted periodically mowed knotweed stands. This difference in management is important as mowing may greatly affect detection success. These sites were chosen because they differed in their landscape context and magnitude of invasion: i.e., the Anse site hosts a very large knotweed population composed of two huge monocultures and many stands of various sizes scattered across the landscape (the total area covered by knotweeds represents 45,772 m²), whereas the Serrières site is only colonized by some stands dispersed along the river (the total area covered by knotweeds represents 3361 m²).

Table 1. Overview of satellite and UAV images used in the classifications for each study site.

Site Name	Latitude	Longitude	Season	Image Acquisition Date		Area of the Pleiades Study Site	Area of the UAV Study Site
				Pleiades	UAV		
Anse	45.936	4.722	Spring	19 April 2016	26 May 2016	213 ha	4.8 ha
			Summer	18 July 2016	<i>Crashed</i>		
			Fall	3 October 2016	22 September 2016		
Serrières	45.319	4.763	Spring	6 April 2016	25 May 2016	263 ha	7.1 ha
			Summer	18 July 2016	<i>Crashed</i>		
			Fall	29 September 2016	5 October 2016		

2.2. Image Preprocessing

The Pleiades images were orthorectified on the Elevation 30 model and projected into the Lambert93 projection system based on the French RGF93 datum.

The two UAV cameras acquired regularly synchronized images with 85% forward and 70% side overlap during flight missions. We georeferenced and mosaicked the images with the photogrammetric software Photoscan v.1.2.6 (Agisoft LLC, St. Petersburg, Russia) using the Structure-from-Motion approach (SfM—[40,41]). SfM produces three-dimensional dense point clouds by identifying common features across scenes from the different angles of the images. Models are then transformed into absolute coordinates using Ground Control Points (GCPs) automatically identified in the images and measured on the ground by Post-Processed Kinematics-GNSS (Trimble Geoplotter 6000—with mean deviation <0.3 m) to ensure georeferencing accuracy. Finally, the point clouds are segmented to generate Digital Surface Models (DSMs) and Digital Terrain Models (DTMs) that are in turn used to orthorectify the mosaics (for further details, see [38,40–42]), producing orthoimages with subdecimetric spatial resolutions.

The automatic generation of the DTMs and DSMs was based on two steps. Firstly, dense point clouds were divided into cells of a certain size (here, 10 m) in which the lowest points were detected. A triangulation of these points was then used to approximate a DTM. Here, to ensure that a maximum of “lowest points” were detected in the various landcovers of our study sites, we used additional UAV images acquired during the previous winter (when plants bore no leaves). Secondly, DSMs were extrapolated by a moving window that compared the remaining points of the clouds with the ground model to assess if their position differed from the ground by a given angle (here, 6°) and distance (here, 1 m) [41].

All data were further georeferenced using additional GCPs to ensure maximal correspondence between dates.

2.3. Classification Design and Variables

In order to evaluate the potential of single- and multi-date imagery for the detection and mapping of knotweeds, several classifications had to be compared. The idea was to assess the benefits of adding some “additional variables” extracted either from the image being classified itself (single-date analysis) or in comparison to an image acquired at another date (multi-date analysis) (Table 2). In other words, for each date and study site, we performed several classifications that differed only by the type of “additional variable” that was (or was not) included in the classifier algorithm.

Table 2. Presentation of the classification design used on each site. The “+” sign indicates that a MBTBR or a CHM is added to the features used to classify the image: e.g., for the *Summer-spring* Pleiades classification, in addition to the features used by Müllerová et al. [35], a MBTBR index calculated between the Summer and the Spring images is used to classify the Summer image.

<i>Classification Name</i>	<i>Image Being Classified</i>		<i>Data Used to Derive “Additional Variable”</i>	<i>Type of “Additional Variable”</i>
Pleiades imagery				
<i>Summer-alone</i>	Summer			-
<i>Summer-spring</i>	Summer	+	Spring	MBTBR
<i>Summer-fall</i>	Summer	+	Fall	MBTBR
<i>Summer-all-dates</i>	Summer	+	Spring + Fall	MBTBR
<i>Fall-alone</i>	Fall			-
<i>Fall-spring</i>	Fall	+	Spring	MBTBR
<i>Fall-summer</i>	Fall	+	Summer	MBTBR
<i>Fall-all-dates</i>	Fall	+	Spring + Summer	MBTBR
UAV imagery				
<i>Spring-alone</i>	Spring			-
<i>Spring-phenology</i>	Spring	+	Fall	MBTBR
<i>Spring-CHM</i>	Spring	+	Spring CHM	CHM
<i>Spring-biCHM</i>	Spring	+	Spring CHM + Fall CHM	CHM
<i>Spring-all-dates</i>	Spring	+	Spring CHM + Fall + Fall CHM	Both
<i>Fall-alone</i>	Fall			-
<i>Fall-phenology</i>	Fall	+	Spring	MBTBR
<i>Fall-CHM</i>	Fall	+	Fall CHM	CHM
<i>Fall-biCHM</i>	Fall	+	Fall CHM + Spring CHM	CHM
<i>Fall-all-dates</i>	Fall	+	Fall CHM + Spring + Spring CHM	Both

There can be many different types of such “additional variables” (especially from multi-date images), such as differences in mean band values, texture, brightness, etc. For computational reasons, we only chose two kinds of variables easily computable by commercial software of image analysis: Bi-Temporal Band Ratios (BTBRs—multi-date information) and Canopy Height Models (CHMs—single- and/or multi-date information).

The BTBR was designed by Dorigo et al. [33] for the very purpose of characterizing the seasonal spectral behaviour of knotweeds by exploiting the phenological variation in the tissue’s chemistry and thus, the radiative responses in the red and green bands at different dates. However in their study, they only worked on two periods (spring and summer) and one of their aerial photographs did not have a *NIR* band. Since they recommended to always use the *NIR* band if possible, and since we worked on three different seasons, we developed a modified version of their BTBR:

$$\text{MBTBR} = \frac{(NIR_y/R_x) - (G_y/G_x)}{(NIR_y/R_x) + (G_y/G_x)}, \quad (1)$$

where *R*, *G* and *NIR* stand for the mean values of the red, green and *NIR* bands, respectively (calculated for each image-object), while the suffix indicates the image the band is from [33]. Here, *x* always designated the image that was being classified, and *y* the image that was not being classified but from which ancillary information was derived. If classifications involved three different image dates (Table 2), three MBTBR indices were computed between each pair of images, where the suffix *x* designated the image that was being classified or the most recent image for the pair that did not include the image being classified.

The CHMs were built by subtracting the DTMs from the DSMs generated during the UAV imagery pre-processing. For this reason, CHMs were only used in the UAV image analysis, for which a CHM was computed for each date. In our analysis, we tested both single- and multi-date CHMs (Table 2). The latter gave information on species growth rates which may be useful to distinguish fast-growing species like knotweeds. Since it was an applied study investigating the potential of CHMs for knotweed detection and not a fundamental study seeking to evaluate the CHM generation

process, only a preliminary accuracy assessment of the CHMs was performed (with a mean error in z-coordinates of 0.25 m calculated from 5 GNSS control-points per site and date of acquisition).

2.4. Classification Procedure

To produce the numerous classifications that had to be compared in this study, we decided to use an object-based approach because, unlike pixel-based methods that only account for the spectral information of images, it also enables the incorporation of scale-dependent structural and contextual information such as the texture, shape or topology of image-objects [43,44]. We thus carried out a multiresolution segmentation with a trial-and-error approach to find the best segmentation parameters for each image. Multiresolution segmentation is a region-merging technique that merges contiguous groups of pixels until a heterogeneity threshold (defined by parameters of scale, shape and colour) is crossed [45]. As emphasized by Müllerová et al. [35], knotweeds lack consistency in their shape and colour. Consequently, we had to operate a very fine segmentation to isolate knotweed-objects from the surrounding background and other plant species, creating tens of thousands of image-objects.

To classify the image-objects, we used the machine learning algorithm Random Forest (RF) that combines multiple classification trees [46]. RF is a non-parametric classifier based on “bagging” (for bootstrap aggregating) that only uses random subsets of training objects and input variables to make decisions, offering several advantages: It is easy to parametrize; computationally efficient; and it is robust to overfitting, correlation between variables, and unbalanced training samples [46,47]. To help the algorithm, we decided to create several thematic classes apart from knotweeds (e.g., water, buildings, trees), that were ultimately merged to only retain three classes: *knotweed*, *cut knotweed* and *other*. For September UAV classifications in Anse, an additional class of knotweed was created (called *island knotweed*) because some knotweeds located on a river shoal had a different appearance than the other stands (probably because they grew on a seasonally submerged shoal).

To train the RF algorithm, training objects visible at every acquisition date were sampled for each class. Since some classes were more abundant than others and since the size of images differed between sites and image-type (satellite or UAV), we could not reach an equal number of samples per class. However, we ensured that each class had between 5 and 30% of its surface selected for training (for *knotweed* classes, the values were between 25 and 30% to ensure globally similar sample sizes across the various classifications).

As we were interested in the effect of MBTBRs and CHMs, we used exactly the same object features (except for, when relevant, the addition of MBTBRs and CHMs) as in Müllerová et al. [35] to be able to compare our results with theirs. These image-object features were: NDVI, statistics on band values (mean, maximum, minimum and normal and circular standard deviations), contrast to neighbouring pixels, geometrical features (area, border length, length/width ratio, asymmetry and compactness) and texture-based metrics (GLCM features of homogeneity, contrast, dissimilarity and entropy in all directions).

All steps of classification were performed in eCognition Developer v.8.9.1 [48].

2.5. Validation and Accuracy Assessment

Four field campaigns in Serrières and six in Anse were conducted in 2016 to cover both study sites in their entirety and thus map all knotweed stands using high-precision GNSS. However, since the ultra-high resolution of UAV imagery often exceeds the precision of the highly time-consuming GNSS measurements [24,49], all mapped polygons were manually corrected through photo-interpretation to ensure sufficient precision matching between the validation datasets and the classification results. Still, many unwanted changes (e.g., shadows, hidden parts of knotweed populations) were displayed across multi-date images due to the imagery characteristics (e.g., timing of acquisition, camera angles, weather conditions), positioning errors, and landscape modifications (e.g., construction, floods, growing vegetation). Therefore, we decided to create an exclusive validation dataset for each date. We also

separated our datasets between “total” and “visible” knotweed populations by manually modifying the validation polygons to remove the parts of knotweed populations that were hidden by trees.

Validation was performed on all knotweed surfaces independent of the training samples (we mapped every square metre of knotweed cover and not just samples), and we computed Producer’s Accuracies (PA; accounting for *errors of omission*) and User’s Accuracies (UA; accounting for *errors of commission*) to evaluate and compare results [50]. Therefore, PA was computed by dividing the correctly classified cover area of the validation dataset (in m²) by the total cover area of knotweed (minus the 25–30% of cover used as training samples), and UA was computed by dividing the correctly classified cover area of knotweed by the total area classified as knotweed [50]. Since knotweeds represented only a small proportion of the total study areas and since we were not interested by other classes than knotweeds, general agreement metrics (e.g., Kappa index, Overall Accuracy) were not computed as they would have been misleading [51–53].

As already mentioned, working with multi-date imagery increases sources of error. In remote sensing, mixed-objects and misregistration issues are usually unavoidable [54,55], but they are enhanced with every addition of data [55]. Consequently, in order to assess the amount of knotweed cover that is missed (i.e., amount of PA reduction) due to these “multi-data” issues, we applied “buffer” boundaries around knotweed predictions to artificially widen them. Predicted objects were thus validated using two types of boundaries, a “crisp” boundary and “buffer” boundaries of two sizes: 2-pixels and 10-pixels (i.e., 16 cm and 80 cm, and 1 m and 5 m for the UAV and the Pleiades images, respectively). In other words, for a 10-pixel “buffer” boundary validation of a UAV classification, any objects within 80 cm of an object predicted as knotweed were classified as knotweed as well. Since we used “surfaces” for validation, “buffer” boundaries necessarily affected UAs (rates of “true-positive” predictions) but not in terms of occurrences (a false prediction is false regardless of its size).

All steps of validation were performed in ArcGIS 10.3 [56].

3. Results

We only present the results for the knotweed populations that were visible from the sky. Indeed, 48.8% and 9% of the total knotweed cover was located under the tree canopy in Anse and Serrières, respectively (and was thus invisible on the images), and was therefore not taken into account. Additionally, due to fresh cutting of knotweed stands at the Serrières site just before several image acquisitions (i.e., all Pleiades images and the fall ones for the UAV), classifications of both Pleiades data and UAV autumn datasets resulted in accuracies below 40% and are thus not presented here.

For the “crisp” Pleiades results (Table 3), the accuracies obtained were relatively weak except for the surprisingly high UA’s for the *cut knotweed* class in the fall classifications (the other results for this class were globally weak; Table S1). For the *knotweed* class, the results are quite comparable between the different spring Pleiades classifications, but using MBTBRs mildly improved UAs. The use of MTBRs also globally improved both PAs and UAs for the fall classifications (the best PA/UA was 61/34% for the Fall-Summer classification).

The UAV classifications reached much higher accuracies than the Pleiades ones (Table 3). In Anse, CHMs and MBTBRs always improved PAs for the knotweed class and usually improved UAs but with less consistency (Table 3). For the UAV-site of Serrières, the addition of CHMs and MBTBRs only had a mildly positive effect on the already high PAs of the *knotweed* class and seemingly no effect on the low PAs of the *cut knotweed* class (Table S2). On the other hand, it led to a very strong increase in UA for both classes at Serrières (Table 3). Except for the *cut knotweed* class at Serrières and *knotweed*’s UA for the spring classification in Anse, all the best results were obtained from using multi-date classification (usually with both CHMs and MBTBRs), and adding CHMs (both single- and multi-date) always improved PAs.

The use of the “buffer” boundaries strongly increased accuracies for both Pleiades and UAV classifications, with PAs often exceeding 80 or even 90% (Table 3). This indicates that, in most cases, the classifier detected the majority of knotweed stands and that the missing parts of the knotweed cover are mostly located on the edges of the detected stands (Figure 2).

Table 3. Classification accuracy assessments for both sites and image types. ‘PA’, Producer Accuracy; ‘UA’, User Accuracy. For details on the characteristics of each classification, see Table 2.

Image Type	Site	Classification Name	Crisp Boundary Results		Buffer Boundary Results	
			PA (%)	UA (%)	2-pixels PA (%)	10-pixels PA (%)
Satellite (Pléiades)	Anse	Summer-alone	59	28	75	88
		Summer-spring	55	28	71	86
		Summer-fall	58	31	74	87
		Summer-all-dates	56	35	72	87
		Fall-alone	50	25	64	81
		Fall-spring	50	25	64	81
		Fall-summer	61	34	77	90
		Fall-all-dates	58	33	74	88
UAV	Anse	Spring-alone	49	56	62	84
		Spring-phenology	57	47	70	84
		Spring-CHM	68	48	81	89
		Spring-biCHM	72	53	84	95
		Spring-all-dates	69	50	82	93
		Fall-alone	46	34	69	92
		Fall-phenology	50	42	68	88
		Fall-CHM	68	37	80	93
UAV	Serrières	Spring-alone	82	48	91	98
		Spring-phenology	81	51	90	98
		Spring-CHM	84	72	92	99
		Spring-biCHM	83	80	91	98
		Spring-all-dates	86	78	93	99

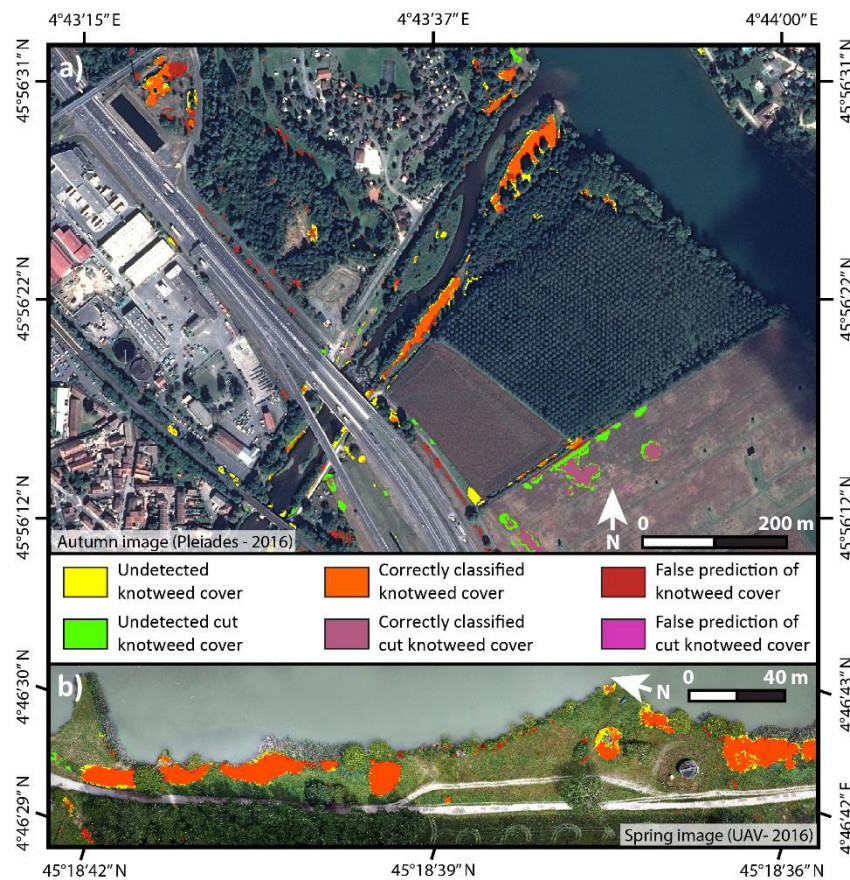


Figure 2. Partial outputs of (a) the *Fall-Summer* classification (Pleiades) of Anse, and of (b) the *Spring-all-dates* classification (UAV) of Serrières. For details on the characteristics of each classification, see Table 2.

4. Discussion

In this study, we assessed the potential of single-date (i.e., spectral, textural and contextual data, CHMs) and multi-date information (i.e., CHMs and MBTBRs) extracted from imagery acquired at different resolutions and time-periods for the detection and mapping of invasive knotweeds with accessible commercial software to make the workflow applicable in ecological conservation. The results show that, for a moderate time and cost investment, knotweeds can now be accurately mapped for operational uses at different spatial scales especially using MBTBRs and UAV-generated CHMs, if not hidden under the canopy of trees or freshly cut. However, the quality of detections strongly depends on the landscape context. To the best of our knowledge, it is the first time UAV-generated CHMs are used to detect IAPs, and our study clearly shows the potential of such an approach.

To date, the literature on knotweed detection using remote sensing is very limited as knotweeds have proven to be quite difficult to distinguish from other plant species. The first attempts were made on aerial photographs and VHR satellite imagery but these studies did not provide quantitative accuracy assessments [34,57], or failed to map the plant due to insufficient population sizes [58]. Dorigo et al. [33], introducing the use of BTBR to quantify the temporal differences in the spectral response of knotweeds, only obtained a PA/UA of 61/7% with their aerial orthophoto and their pixel-based approach using the RF classifier. More recently, Michez et al. [36] tried to map the distribution of three IAPs (including knotweeds) using an object-based approach on UAV orthophotos. They admitted failing at reaching satisfying results, notably because their late-fall images included too many projected shadows [36]. Müllerová et al. [35], on the other hand, compared UAV and Pleiades images acquired at different dates and classified with different algorithms to evaluate the best trade-offs between spectral, spatial and temporal resolutions for operational applications. Their pixel-based analysis gave the best PAs/UAs of 74/95% for a July Pleiades image (50 cm) with a RF classifier, and of 82/83% for a November UAV image (which allowed them to detect some under-canopy knotweed populations) resampled to a 50 cm spatial resolution and classified with a Maximum Likelihood classifier. For the satellite analysis, they consequently obtained better accuracies than our best “crisp” Pleiades results. With the UAV imagery, however, our best “crisp” PA results were comparable to (Anse site) or outperformed (Serrières) the results of Müllerová et al. [35]. Compared to the late autumn imagery used in Müllerová et al. [35], using images from late-spring/early-fall provides opportunities for better image acquisition due to an extended season for collection and better weather conditions. Our proposed methodology therefore enables the accurate mapping of knotweeds any time during the growing season, which could be valuable for practical management applications.

The mentioned differences in accuracies among the study sites are likely due to their landscape context. Both single- and multi-date detection of knotweeds is easier in open landscapes such as the Serrières site (i.e., a riverside recreational open lawn), where the plant grows in well-shaped stands distinct from the background. In more complex landscapes, where the nature and size of real objects is highly heterogeneous, classification errors due to mixed-pixels or mixed-objects increase [59]. Detection of knotweed stands in semi-natural riparian areas like Anse and the Czech site of Müllerová et al. [35] was, therefore, likely impeded by the heterogeneous cover that included many shadows, mingled-vegetation, and growing shrubs and trees. Fortunately, knotweeds do not commonly grow inside closed forests [60]; large forest populations like the one in Anse being extremely rare. Our results indicate that in such landscapes dominated by a highly heterogeneous vegetation cover, the use of CHMs (single- or multi-date) brings substantial accuracy improvements. CHMs are rarely used to map IAPs, especially herbaceous species (but some authors have used LiDAR-based CHMs to map woody plants (see Reference [61])). It is surprising since CHMs, whether single- or multi-date, should be particularly useful to reduce confusion between trees (or shrubs) and fast-growing herbaceous species (e.g., [62,63]). This is supported in our study, as the accuracy gained from the CHMs at the Serrières site, which was composed mostly of grass and fast-growing forbs like knotweeds or reeds, was weaker than at the wooded site of Anse (Table 3). Since it is the first time UAV-generated CHMs are used to map the distribution of an IAP and since no accuracy assessment of the CHMs themselves has

been made, errors in CHMs likely exist and improvements in the methods can certainly be undertaken. Nevertheless, CHMs improved results in all of our classifications (Table 3).

Our “buffer” boundary results outperformed by far those obtained by any other study. While it is reasonable to assume that “buffer” boundaries partly included knotweed cover that would never have been classified as such by the classifier (i.e., only by chance), it also likely compensated for a substantial portion of the mis-registrations and mixed-objects at the edge or within knotweed stands due to the use of multi-date imagery (Figure 3). Such inevitable errors are indeed enhanced with every addition of data (e.g., image, spectral band, CHM). In Figure 3a, for instance, visible knotweed cover changes across dates due to floods or long projected shadows. In Figure 3b,c, image-objects circled in red are homogeneous on the spring image but not on the fall one because of the growing vegetation and the spectral and positional registration inaccuracies between images. Such image-objects (all knotweeds) would have different heterogeneous spectral or textural responses, and would thus probably be classified differently in multi-date classification, leading to patchy detection and mapping of numerous image-objects at the edge or within stands. In other words, even if CHMs and MBTBRs improve discrimination of image-objects that are homogeneous across all dates, they artificially reduce the accuracy of image-objects that are heterogeneous across dates because they are too different from the training samples chosen on the homogeneous objects. CHMs derived from SfM procedure also show imprecisions in areas of very dense canopy (average XYZ errors ranging from 3 to 14 cm) due to the lack of visible ground, leading to some inaccuracies in CHMs. Mis-registrations were further enhanced by the difficulty of finding suitable GCPs across imagery in semi-natural areas due to the lack of “fixed” elements: e.g., constructions, rocks. These assumptions are supported by the fact that, even with weak “crisp” PAs, most of the 10-pixels “buffer” PAs reached or exceeded 90–95%. This means that in most cases, the vast majority of the “omitted” knotweed cover lies in the direct vicinity of detected stands (as shown in Figure 2), but that “crisp” accuracy assessments are too conservative to capture the full extent of knotweed image-objects. On balance, “buffer” boundaries may be more useful for end-users primarily interested in PAs, such as land managers or conservation scientists, while the information given by “buffer” boundaries may be less relevant for end-users whose purpose is to build prediction models as they may be more interested in UAs.

Our “buffer” boundary results actually provide useful information to the end-user by rationalizing PAs that would otherwise be unfairly low for practical use; see Reference [54]. Using such an approach lowers the likelihood of knotweed omission that is of interest for eradication measures. Moreover, these “buffer” boundaries may well represent reasonable distances of prospection during field surveys, i.e., end-users monitoring/eradicating knotweed stands using remote sensing predictions will most probably include a few centimetres to metres around the predicted location to their survey. To illustrate, a PA/UA of 98/80% with an 80 cm “buffer” boundary (i.e., like our *Spring-biCHM* classification in Serrières) means that if one goes and checks just 80 cm around every location predicted as knotweed, one will actually find 98% of the knotweed cover of the study area visible from the sky and only get 20% of “false-positive” predictions (adding a buffer zone around a false prediction does not make it any truer, and therefore changes of UA due to “buffer” boundaries are not relevant).

The choice of the most appropriate approach and imagery, therefore, varies with the purpose of the classification (e.g., land management, biodiversity conservation, research on biological invasions), the type of landscape, and the scale of the target area. For regional scales, the use of VHR satellite imagery is the only reasonable option. In such a case, the pixel-based approach of Müllerová et al. [35] may be more appropriate than object-based classifications because at this resolution, knotweed stands lack distinctive features. Still, adding MBTBRs in the classification workflow could likely improve the results. If single-date analysis is chosen, the image should preferably be acquired during early summer when knotweeds are at their full-height and projected shadows are the shortest (e.g., Figure 3a) or, if the weather allows it, at the late autumn senescent stage, as suggested by Müllerová et al. [35]. At the local scale, for simple and open landscapes, UAV single-date images could work well, but good results can also be achieved with spring images with single- or multi-date analyses (Table 3).

For more complex and heterogeneous landcovers, the use of at least two-date MBTBRs and/or CHMs is strongly recommended if images cannot be acquired during the senescence stage where knotweeds are most distinctive [35], which is likely in regions where autumns are characterized by cloudy conditions. CHMs should be particularly useful in heterogeneous vegetation to help distinguish between herbaceous and woody species [62,63].

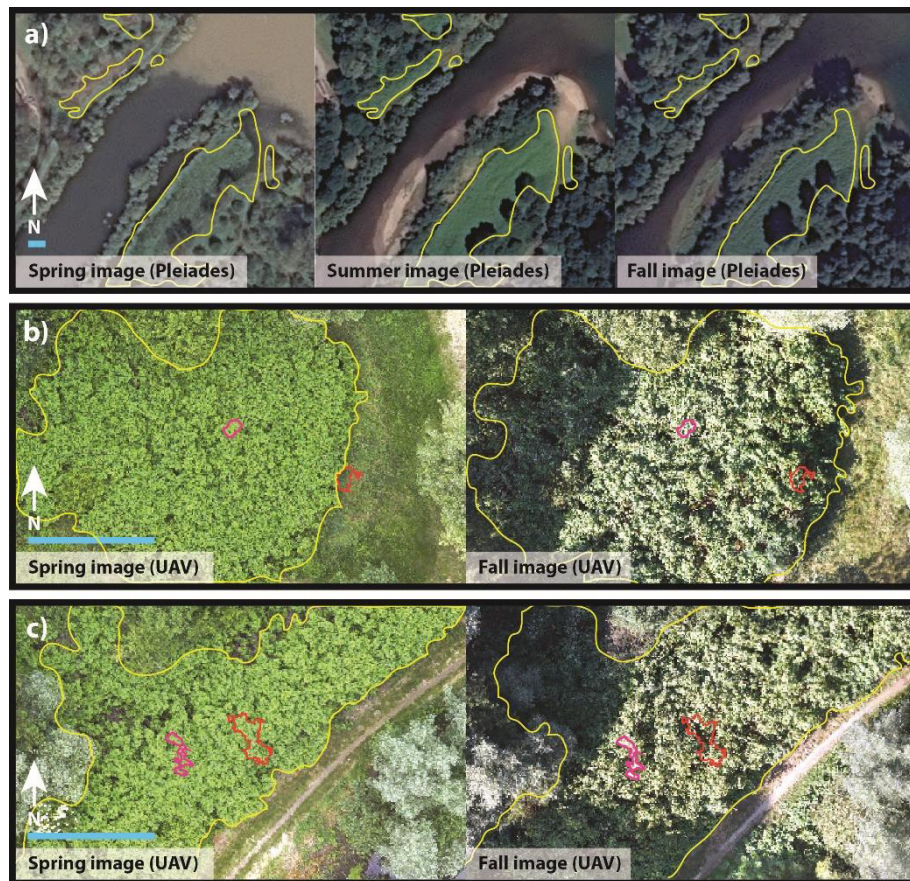


Figure 3. Illustration of some sources of errors due to the use of multi-date imagery, linked to (a) changing landcover, (b) positional misregistration and (c) mixed-objects. The blue scale-bar represents a length of 8 m. The red and pink lines delineate image-objects generated by the multiscale segmentation process. The yellow lines delineate the outlines of the knotweed populations for each date.

5. Conclusions

We showed that the highly problematic knotweeds can be accurately mapped (i.e., false positive and true positive error rates often below 10–15%) from both satellite and UAV imagery, particularly when using multi-date band ratios and Canopy Height Models (CHMs). The proposed methodology provides a powerful tool in invasive alien plants (IAPs) management, with high accuracy and a straight-forward approach assuring its operational use. Proposed automated detection of one of the most problematic IAP in Europe and North America can increase the effectiveness of eradication measures as well as reduce the costs of expensive field campaigns, enabling early detection, regular monitoring and assessment of control measures. The results showed that it is possible to detect very small knotweed stands as long as they cover areas larger than 4–5 pixels and are visible from above. However, plants growing under the tree canopy, or that are freshly cut, remain excessively hard to detect.

Regardless of the chosen method, end-users should be aware of both limitations and improvement perspectives. The pre-processing procedure of UAV images is relatively straightforward but still requires some technical expertise and, as a new technique, is undergoing rapid development (see

References [38,40]). UAVs are also sensitive to weather hazards and constraining legal regulations [7]. For both satellite and UAV imagery, the quality of imagery influences the choice of the data to be classified and the number of classes to be created. Wrong timing of data acquisition is a frequent issue (e.g., if the target species has been freshly cut or eradicated), though detection may still be feasible (e.g., if knotweeds had some time to regrow). On the other hand, easy improvements of accuracy could be obtained from masking out unlikely locations using GIS expert-systems, improving surface reflectance calibration, and using multi-date segmentation and texture analysis (at the expense of computational time). Incorporating UAV-embedded LiDAR to account for errors in z-coordinates and thus improve the accuracy of CHMs could also likely increase detection accuracies. Finally, another promising approach would be the use of hyperspectral imagery. For many years, the cost and spatial resolution of hyperspectral satellite or airborne imagery was unfit for the detection of herbaceous species. However, UAV-borne hyperspectral solutions are now emerging and give interesting results for the monitoring of plants [64,65]. Further research on the use of such technologies for knotweed detection should certainly be undertaken although their expertise requirements would be a deterrent for many potential end-users.

Supplementary Materials: The supplementary materials are available online at <http://www.mdpi.com/2072-4292/10/10/1662/s1>.

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– CHAPTER FIVE: DISCUSSION –

The previous chapters of this thesis have addressed various points related to the study of the spatiotemporal dynamics of knotweeds at different scales. After the contextualisation of the introductory Chapter, Chapter Two offered an opportunity to witness the tolerance and resilience of regenerating knotweed clones, and to observe that these juvenile plants are able to adopt different growth forms and, possibly, to operate trade-offs in their clonal architecture and space colonisation in order to adapt to the variability of environmental conditions. In Chapter Three, we have seen that the expansion of established stands of knotweeds is mostly affected by their own size and the proximity of obstacles and sources of disturbance, although competition for light might also play a role. We also showed that low-frequency mowing was quite ineffective to slow down their lateral expansion and we provided evidences that knotweeds could have the potential to colonize and thrive at high elevation. In Chapter Four, we proposed a way to help resolving the problem of large-scale data acquisition by using remote sensing techniques to accurately map knotweeds. Results were promising but we also highlighted that remote sensing is not devoid of limitations.

Each of these humble contributions helped improving our understanding of the invasion dynamics at different scales, or helped to acquire tools to reach such a goal. Yet, as insightful as these chapters might have been, they only offered a limited view on some small clogs in the gigantic mechanism that are the spatiotemporal dynamics of knotweeds. To create more links between these studies and put them into perspective, we integrated our work within the vast knowledge that can be gleaned here and there on the spatiotemporal patterns and underlying processes of knotweeds invasion.

This is the aim of the following review article proposed as Discussion for the thesis.

5. THE SPATIOTEMPORAL DYNAMICS OF A STRONG INVADER: A REVIEW ON KNOTWEEDS (*REYNOUTRIA SPP.*) INVASION PATTERNS AND PROCESSES ACROSS SCALES

(Article in preparation for submission in *Biological Reviews*)

5.1. INTRODUCTION

Invasive non-native plant species (INPSs) are a major component of global change (Vilà *et al.*, 2011; Simberloff *et al.*, 2013), and understanding their driving forces is one of the most pressing challenge for modern ecologists. In order to assess the effect of INPSs on biodiversity and ecosystem functioning, to predict their future spread and interactions with other aspects of global change, and to implement efficient management measures and policies, we must identify what processes underpin their invasion dynamics (Mack *et al.*, 2000; Theoharides & Dukes, 2007; Catford *et al.*, 2009).

Despite many efforts, our progression towards high predictability of the invasion dynamics of INPSs has been slow (Kolar & Lodge, 2001; Dietz & Edwards, 2006; Heger *et al.*, 2013). One reason for this situation is that dynamics of invasion are often highly species-specific (Pauchard & Shea, 2006; Gurevitch *et al.*, 2011). Another is that invasions are not linear processes controlled by a few drivers acting in a monotonous fashion across space and time (Dietz & Edwards, 2006; Theoharides & Dukes, 2007). Invasions are actually controlled by a hierarchy of processes occurring simultaneously at different spatiotemporal scales, where each level of this hierarchy is potentially influenced and structured by what happens at other scales (Levin, 1992; Pyšek & Hulme, 2005; Pauchard & Shea, 2006). The scale of most ecological studies is not wide enough to describe such intertwined dependencies (Wiens, 1989; Pyšek & Hulme, 2005; Pauchard & Shea, 2006) and the need for multiscale studies is increasingly acknowledged (Wiens, 1989; Pyšek & Hulme, 2005; Pauchard & Shea, 2006; Pauchard *et al.*, 2009; Gurevitch *et al.*, 2016). As the range of spatial and temporal scales relevant to account for all processes underlying invasion dynamics may be too large to be encompassed in any single study, meticulous literature reviews may alternatively be used.

Many INPSs are still challenging the knowledge and means of action of scientists and stakeholders (Early *et al.*, 2016). The complex of species known as knotweeds (*Reynoutria* spp.; *Polygonaceae*) certainly belongs to these INPSs. This name refers to Japanese knotweed (*Reynoutria japonica* Houttuyn [syn. *Fallopia japonica* (Houttuyn) Ronse Decraene, *Polygonum cuspidatum* Siebold & Zuccarini]), Giant knotweed (*Reynoutria sachalinensis* (F. Schmidt) Nakai [syn. *Fallopia sachalinensis* (F. Schmidt) Ronse Decraene, *Polygonum sachalinense* F. Schmidt]), their hybrid Bohemian knotweed (*Reynoutria x bohémica* Chrtek & Chrtková [syn. *Fallopia x bohémica* (Chrtek & Chrtková) J. P. Bailey, *Polygonum x bohemicum* (Chrtek & Chrtková) Zika & Jacobson]), and any other crosses or backcrosses between these taxa and other related species (Bailey *et al.*, 2009). Hereafter, we will use the generic name “knotweeds” when referring to all taxa together and the Latin names when referring to a

specific *Reynoutria* taxon. Introduced from eastern Asia during the 19th century as ornamental and fodder plants, knotweeds are now widespread in Europe and North America (Alberternst & Böhmer, 2006; Bailey & Wisskirchen, 2006; Barney, 2006), and present or locally abundant in Australia (Ainsworth *et al.*, 2002), New Zealand (Howell & Terry, 2016), South Africa (Germishuizen, 1986) and Chile (Saldaña *et al.*, 2009; Fuentes *et al.*, 2011)(Figure 1). Knotweeds are fast-growing rhizomatous geophytes that form dense monoclonal stands (a.k.a. patches) that may reach 4-5 meters in height (depending on the species) and cover several hundreds of square meters (Beerling *et al.*, 1994; Barney *et al.*, 2006; Bailey *et al.*, 2009). Their success may lead to strong modifications of ecosystem properties, and often cause security or accessibility issues along rivers or anthropic amenities (Child & Wade, 2000; Alberternst & Böhmer, 2006; Lavoie, 2017). Although the extent of knotweeds' impacts is increasingly debated (e.g. Lavoie, 2017; Davis *et al.*, 2018; Fennell *et al.*, 2018), they still represent a problem for many stakeholders and managers, and are exceedingly difficult to eradicate (McHugh, 2006; Delbart *et al.*, 2012). Consequently, their annual invasion costs exceed £160 million year⁻¹ in the UK alone (Williams *et al.*, 2010), and are considered to be among the worst INPSs in the world (Lowe *et al.*, 2000).

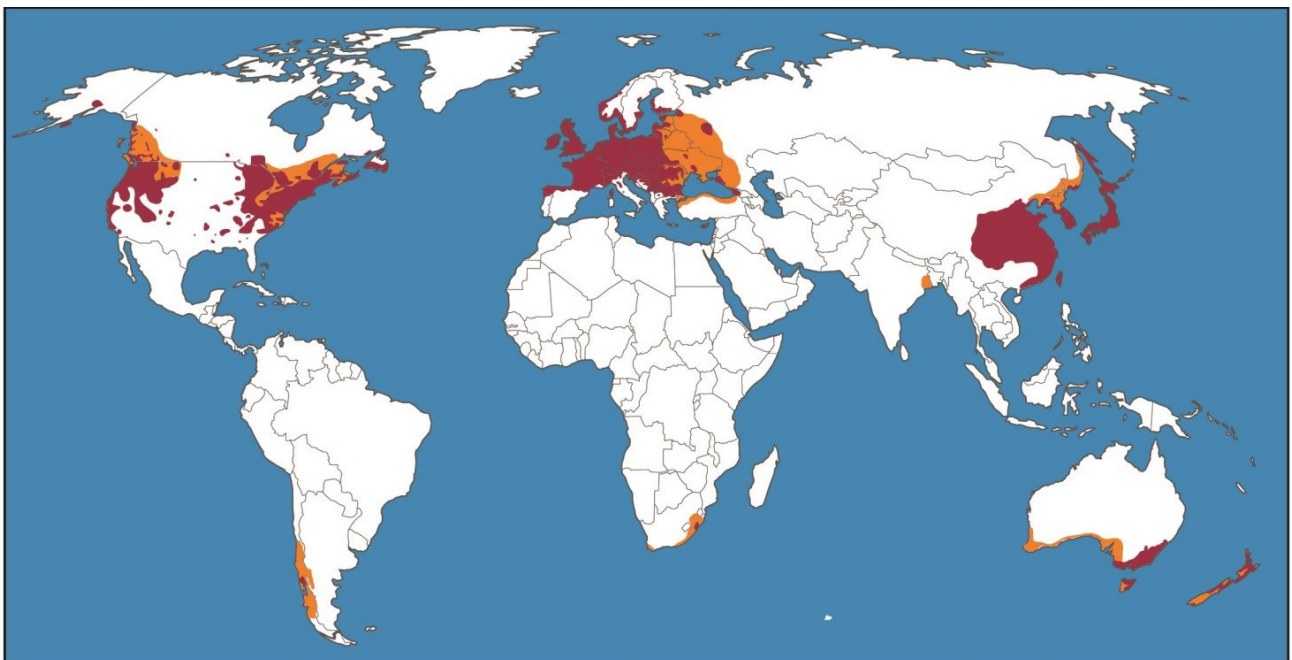


Figure 1. Worldwide distribution of the knotweed complex (red). Areas where the distribution of knotweeds is likely underestimated are also displayed (orange). This map was created by using published records of knotweeds as well as various internet sources [Robinson projection].

After having awed the horticultural world for nearly a century (Townsend, 1997; Bailey & Conolly, 2000; Del Tredici, 2017), knotweeds have become a subject of scientific study for at least 60 years (e.g. Fuchs, 1957). With more than 300 references in the scientific literature in English and French alone, and countless technical reports and webpages, knotweeds are probably one of the most studied INPS worldwide. Despite all these research and communications, their management is still an unresolved issue (Delbart *et al.*, 2012; Braun *et al.*, 2016), perception and control recommendations are often contradictory (Cottet *et al.*,

2015; Robinson et al., 2017a; Robinson et al., 2017b), and a full depiction of their spatiotemporal dynamics across scales as well as their causes and consequences is still missing.

Only a few number of studies explicitly approached the question of the spatial dynamics of knotweeds, especially at the local or individual scale (Tiébré et al., 2008; Martin et al., 2019). Still, many useful insights on the matter may be gained from other studies. The aim of this paper is to: (i) review the current knowledge on the spatial and temporal patterns of knotweeds and their underlying processes across scales; (ii) highlight what drivers affect these processes at each scale and how processes interact between scales; and (iii) explore what this information implies in terms of management improvement and research perspectives. The idea is to draw up an actualized portrait of the full invasion dynamics of knotweeds useful for both applied and basic research.

Following Wiens (1989) and unlike geographers, we refer to the size of scales in a general sense: e.g. a large scale covers a large extent.

5.2. THE MICRO-LOCAL SCALE

Whatever the scale, plant invasions begin with propagules arrival. The first colonization of a continent by an INPS or the fine scale advance of an invasion front, both require that a propagule arrives and gives birth to a functioning plant. If the spatiotemporal dynamics of propagules may span a wide range of scales (see section 5.4.1.), the drivers of the immediate dynamics of a propagule's outcome (i.e. a juvenile; Table 1) only act on a particular scale that we will refer to as the micro-local scale. The micro-local scale is the scale of a plant establishment. The range of the spatial and temporal dimensions of plant establishment is of course species-specific but, in the case of knotweeds, it is globally small: i.e. the success or failure of establishment is determined quickly and by very local drivers. The grain and extent (cf. O'Neill et al., 1986; Wiens, 1989) of the spatial dimension of the micro-local scale cover an area comprised between the surface covered by the establishing plant and a few square meters (i.e. maximum area in which other objects are close enough to substantially affect the juvenile's survival or performances; e.g. by modifying the microclimate or light availability).

Establishment may be divided into three stages (Richardson et al., 2007): colonization, survival, and growth to maturity. For clonal INPSs like knotweeds, the nature of the considered propagule (a seed enclosed in an achene, a rhizome fragment, or a stem fragment) will have strong influence on the outcome of the establishment process.

5.2.1. The colonization process

5.2.1.1. *Viability and germination of knotweed seeds*

For decades, the germination and seedling establishment of knotweeds in their introduced range was thought to be insignificant or non-existent (Bailey, 1994; Seiger, 1997). We know

now that knotweeds do reproduce sexually and that seeds (mostly of hybrid origin) germinate in the wild (Forman & Kesseli, 2003; Grimsby *et al.*, 2007), even though seedling establishment remain relatively rare (Tiébré *et al.*, 2007b; Bailey *et al.*, 2009). Still, since limited seed recruitment in clonal plants is generally sufficient in the long-term to maintain the advantages of genetic diversity (Eriksson, 1997; Fischer & van Kleunen, 2001), the potential of knotweeds' seedling establishment is a component of their invasiveness that should not be neglected.

Term or concept	Definition	Further reference(s)
Clonal fragment	<i>A group of physically interconnected ramets of a clone</i>	de Kroon & van Groenendael (1997)
Dispersal	<i>The process of movement of organisms between locations</i>	Pauchard & Shea (2006)
Juvenile	<i>A young plant (born either from sexual or vegetative reproduction) that still lacks all the characteristics of an adult individual</i>	-
Landscape	<i>A spatially heterogeneous area whose extent depends on the ecological process, species, or species' organizational level under investigation</i>	Wiens (1989); With (2002); Gurevitch <i>et al.</i> (2016)
Metapopulation	<i>Ensemble of all regional populations interconnected through long-distance dispersal, regardless of the frequency of these gene fluxes</i>	Ehrlén & Eriksson (2003); Murphy & Lovett-Doust (2004)
Population	<i>A group of individuals of the same species close enough to experience relatively similar environmental conditions and to potentially maintain direct interactions</i>	Camus & Lima (2002); Gurevitch <i>et al.</i> (2016)
Ramet	<i>The smallest unit of a clonal plant that may be physiologically independent; usually a stem and its associated roots</i>	de Kroon & van Groenendael (1997)
Regenerating ramet	<i>A juvenile plant born from a vegetative propagule (a rhizome or a stem fragment)</i>	-
Stand	<i>A knotweed's organizational level composed of two or more closely aggregated (or intertwined) clonal fragments, not necessarily of the same knotweed taxa, that seem to belong to the same clonal fragment (a.k.a. patch)</i>	Martin <i>et al.</i> (2019)
Seedling	<i>A juvenile plant born from a seed</i>	-

Table 1. Glossary of the potentially ambiguous terms and concepts used in this review.

The rarity of knotweed seedling recruitment is hardly explained by a low seed viability or germination potential. In autumn, after fructification, seeds in their achenes have to stay attached to their parents without enduring early-frost to become viable, before being dispersed and overwintering in a state of dormancy until spring (Bailey, 1994; Beerling *et al.*, 1994; Nishitani & Masuzawa, 1996). Additionally, the parents have to grow in an area with at least 2505 degree-days for the seeds to be viable (Beerling, 1993; Groeneveld *et al.*, 2014). During its dormancy, a seed may be attacked by predators (Engler *et al.*, 2011) or may rot in the soil in case of a mild and humid winter (Tiébré *et al.*, 2007b; Bailey *et al.*, 2009; Funkenberg *et al.*, 2012). If not, it may germinate. Depending on environmental conditions, knotweed seeds have mean germination rates ranging between 48 and 100% (Adler, 1993; Mariko *et al.*, 1993; Seiger, 1993; Bailey, 1994; Maruta, 1994; Forman & Kesseli, 2003; Zhou *et al.*, 2003; Bram & McNair, 2004; Tiébré *et al.*, 2007b; Engler *et al.*, 2011; Funkenberg *et al.*, 2012; Groeneveld *et al.*, 2014). Such globally high germination rates possibly vary with seed maturity (Bram & McNair, 2004; Engler *et al.*, 2011) and the considered genotype. Knotweed seeds and seedlings are well-adapted to cold and temperate environments (Maruta, 1976; Mariko *et al.*, 1993; Maruta, 1994; Funkenberg *et al.*, 2012; Holle & Tsuyuzaki, 2018) but they

do not tolerate droughts (Maruta, 1976; Funkenberg *et al.*, 2012). Interestingly, germination can occur directly in water (Lamberti-Raverot *et al.*, 2019). Finally, germination in itself is not prevented by reduced light availability (Funkenberg *et al.*, 2012; Holle & Tsuyuzaki, 2018), but other components of competition may reduce germination rates (Popovici *et al.*, 2011; Rouifed *et al.*, 2018b).

5.2.1.2. Regeneration potential of knotweed fragments

Since fragment dispersal (Table 1) is recognized as the main mean of knotweed spread (Pyšek & Prach, 1993; Barney *et al.*, 2006), the regeneration potential of knotweed's fragments has been extensively studied over the years, especially in Europe. Knotweeds exhibit very impressive regeneration abilities. Although regeneration from internode tissues (Locandro, 1973), or even leaves (Brabec & Pyšek, 2000) have been observed, regeneration usually requires fragments with at least one node (even cut in half) (de Waal, 2001; Sásik & Eliáš, 2006) and thus, an axillary meristem.

In controlled conditions, new plants have been repeatedly produced from rhizome fragments weighing < 1 g (Brock & Wade, 1992; Child, 1999), and the regeneration rate as well as the vigour of the juveniles quickly increase with the size of both rhizome (Beerling, 1990; Adler, 1993; Child, 1999; Sásik & Eliáš, 2006) and stem fragments (Brock *et al.*, 1995; Child, 1999; Child & Wade, 2000; de Waal, 2001). For rhizomes, 100% regeneration rates may be reached with fragments of less than 10 cm (Child, 1999). Overall, *R. x bohemica*'s rhizomes regenerate better than *R. japonica*'s that do better than *R. sachalinensis*' (Brabec & Pyšek, 2000; Bímová *et al.*, 2003; Rouifed, 2011), and rhizome fragments have much higher regeneration rates than stem fragments (Brock *et al.*, 1995; Child, 1999; Brabec & Pyšek, 2000; Bímová *et al.*, 2003). There is controversy about which taxon possesses the best stem regeneration abilities (Child, 1999; Bímová *et al.*, 2003), but *R. sachalinensis* is the only one whose stem fragments regenerate as well as its rhizome's (Bímová *et al.*, 2003). Interestingly, the regeneration abilities of *R. x bohemica* may have a genetic component (Pyšek *et al.*, 2003; Rouifed, 2011; Lamberti-Raverot, 2016), but it was not found or investigated for the parental taxa (Pyšek *et al.*, 2003). It is noteworthy because it appears that the most widely distributed hybrid genotypes in Czech Republic are also those that have the highest regeneration rates, suggesting that this feature is highly important for the invasion success of the species (Pyšek *et al.*, 2003; Mandák *et al.*, 2005).

In natural conditions, rhizome fragments appear to regenerate as well in meadows as in greenhouses (Brabec & Pyšek, 2000), but the regeneration from stem fragments is affected by shade (Child, 1999). Competition with natives, especially if they are functionally similar, also decreases the vigour of the hybrid juveniles born from fragments (Rouifed, 2011). The regeneration of stem fragments appears to be increased when they spent some time in water, and the regeneration potential of *R. x bohemica*'s rhizomes only declines when submerged for more than 28 days, potentially highlighting the role of hydrochory in the evolutionary history of knotweeds (Brock & Wade, 1992; Child, 1999; Bímová *et al.*, 2003; Lamberti-Raverot, 2016). Knotweeds regeneration from fragments is also affected by edaphic properties, with lower regeneration rates in poor soils (Bímová *et al.*, 2003; Rouifed, 2011) and even inhibition

in some substrates (Navratil *et al.*, 2018), possibly as a result of allelopathic effect from other plants, as demonstrated for *R. sachalinensis* (Parepa *et al.*, 2014) but not *R. x bohemica* (Christina *et al.*, 2015). Conversely, it has been suggested that allelochemicals exuded from nascent *R. x bohemica* may cause native soil biota to enhance rhizome regeneration (Parepa *et al.*, 2013), but this could only be true in nutrient-rich soils (Parepa & Bossdorf, 2016). Floods or earth-moving activities may also bury many knotweed fragments, with of course impacts on their regeneration success. Still, regenerations from 2 m deep rhizome fragments have been witnessed (Alberternst & Böhmer, 2006), and Francis *et al.* (2008) have shown that although shallow burial (< 25 cm) does not prevent regeneration from *R. japonica*'s fragments, increasing burial depth quickly affect the vigour of juveniles and that a threshold (dependant on the size/weight of fragments) must exist beyond which regeneration is no longer possible.

5.2.2. Survival of knotweed juveniles

The previous sections have highlighted that the rates of knotweed seed germination and fragment regeneration are frequently very high. Still, in the wild, establishment success varies greatly between the three sorts of propagules (achene, stem, and rhizome) because environmental variables do not have the same impact on their probability of survival. Seeds have to produce fully functional individuals from almost nothing, stem fragments have limited reserves and only a few meristems, while rhizome fragments may contain huge amount of reserves and may already possess a large bud bank. These differences naturally play a decisive role in the likelihood of knotweed establishment.

A knotweed juvenile that had the chance to rise from a seed in spring must quickly develop its organs to face the various environmental conditions of its first year. On the volcanic deserts of Japan, it has been shown that seedlings of *R. japonica* var. *compacta* must develop deep roots before summer in order to survive summer droughts (Maruta, 1976). Similarly, by the end of the growing season seedling rhizomes must have produced enough suber and accumulated enough starch to avoid winter mortality (Maruta, 1983, 1994). Consequently, the survival rate of seedlings decreases with the shortening of the growing season and thus, elevation (Maruta, 1994; Nishitani & Masuzawa, 1996; Holle & Tsuyuzaki, 2018), to reach only 2% at 2500 m a.s.l. on Mt. Fuji (Maruta, 1994). In the lowlands and in their introduced range on the other hand, seedlings experience very different conditions than on the high slopes of volcanoes, but cold-limitation likely occurs as well. As knotweed seedlings have a low growth rate, they are easily outperformed by other plant species (Bailey, 2003; Rouifed, 2011; Funkenberg *et al.*, 2012; Christina *et al.*, 2015). Competition could directly provoke the death of seedlings or indirectly prevent them to produce enough biomass to overwinter. Additionally, seedlings are highly vulnerable to late spring frosts (Funkenberg *et al.*, 2012), soil dryness (Beerling *et al.*, 1994), water saturation (Funkenberg *et al.*, 2012) and, in their native range, herbivory (Kawano *et al.*, 1999; Bailey, 2003; Maurel *et al.*, 2013). It is also likely that seedlings would not endure temperatures that are too high. Because of this high vulnerability, it is reasonable to think that seedlings establishment only occurs on very

discrete occasions (*windows of opportunity*, see Myster, 1993), probably after severe disturbances that destroy competitors and may induce nutrient pulses (cf. Bailey, 2003; Bailey & Spencer, 2003), as suggested for other clonal species (Eriksson, 1997). Still, these occasional establishments are sufficient to maintain a regionally high genetic diversity of the hybrid progeny (Gaskin *et al.*, 2014; Buhk & Thielsch, 2015; Bzdega *et al.*, 2016), and therefore to select for more adapted genotypes.

The long-term survival of knotweed juveniles born from fragments has seldom been purposely investigated, but the numerous studies on their occurrences and ecological preferences enlighten us on the broad tolerance of knotweed stands and thus, partially, also on the one of regenerating ramets. Knotweeds may indeed grow on various soil types (e.g. sand, loams, peat, alluvial and colliery soils, clay, shingles) with a wide range of nutrient levels, pH, granulometry, and organic matter content (Locandro, 1973; Palmer, 1990; Beerling *et al.*, 1994; Palmer, 1994; Barney *et al.*, 2006). Knotweeds are even able to establish on soils with high concentrations of Sulphur dioxide (Beerling *et al.*, 1994 and references therein), salt (Richards *et al.*, 2008; Rouifed *et al.*, 2012), heavy metals (Berchová-Bímová *et al.*, 2014; Sołtysiak & Brej, 2014; Michalet *et al.*, 2017), and allelopathic compounds (Rouifed, 2011; Christina *et al.*, 2015). However, the survival of juveniles seems to be impeded by low soil humidity and droughts (Conolly, 1977; Marigo & Pautou, 1998; Schnitzler & Müller, 1998; Tiébré *et al.*, 2008; Descombes *et al.*, 2016), and likely by extreme temperatures (Beerling *et al.*, 1994; Baxendale & Tessier, 2015). The effect of disturbances and competition on regenerating ramets is more variable and likely depends on the size of the fragments they are born from. Some authors suggest that very frequent disturbances prevent knotweed establishment (Beerling, 1991; Bímová *et al.*, 2004; Tiébré *et al.*, 2008), and Brabec & Pyšek (2000) found that the survival of knotweed juveniles was significantly affected by mowing and grazing. On the other hand, using larger rhizome fragments, various studies showed that juveniles of *R. japonica* were resilient to at least three aerial shoots' destruction events per year (Seiger & Merchant, 1997; Gowton *et al.*, 2016; Martin *et al.*, in prep.). Seiger (1993) showed that the survival rate of *R. japonica*'s juveniles was significantly lower in forest understorey compared to open riverbanks. However, many authors report that strong competition for light does not prevent knotweeds' establishment (Beerling, 1990; Duquette *et al.*, 2015; Descombes *et al.*, 2016; Dommanget *et al.*, 2016; Dommanget *et al.*, 2019; Martin *et al.*, 2019; Martin *et al.*, in prep.), probably because large fragments of rhizomes have likely enough reserves to maintain growth even in stressful environments.

5.2.3. Establishment success and growth to maturity

The previous sections highlight the duality of the environmental tolerance of young knotweeds between sexually-born and vegetatively-born juveniles. If environmental filtering exerts a very strong pressure on knotweed seedlings, juveniles born from fragments (especially from rhizomes) are very tolerant and resilient. Moreover, knotweeds' establishment potential is strongly constrained by the size/weight of clonal propagules. Most experimental studies tested regeneration and survival on fairly small rhizome fragments (<

15 g). It is rather curious seeing that knotweeds may produce kilograms of rhizomes per square metres (e.g. Callaghan *et al.*, 1981) and since nothing indicates that dispersed rhizomes in the wild should be particularly small. Above-mentioned evidences then suggest that juveniles born from rhizomes may, given a sufficient fragment size/weight, survive and establish in most temperate terrestrial habitat. Actually, the only conditions that undeniably prevent knotweed establishment are prolonged soil dryness or water saturation. Due to the paramount importance of establishment for larger scale spatiotemporal dynamics, these considerations are highly important for the management and prediction of knotweed invasions. For instance, the width of knotweeds' environmental niche (see section 5.4.2.) and the invasibility of forested habitats should not be underestimated (Figure 2).

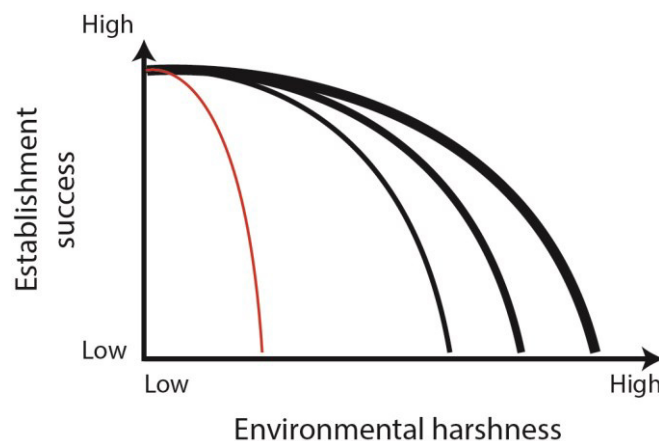


Figure 2. Theoretical depiction of knotweeds' establishment success as a function of environmental harshness, as suggested by the literature. The red curve represents seedlings while the black curves represent regenerating ramets born from vegetative fragments of increasing weights/sizes (represented by increasing line thickness).

A key problem in the analysis of knotweed establishment is that it is a fuzzy concept whose limits are not clearly defined. Richardson and colleagues (2007) propose that establishment is complete when the plant reach maturity. If maturity is being able to produce flowers and seeds, then knotweed seedlings and regenerating ramets reach maturity within their first growing season (Forman & Kesseli, 2003; Martin *et al.*, in prep.), even when ramets are growing under heavy shade (Martin *et al.*, in prep.). However, knotweed survival is mostly measured after a few weeks or, at best, after their first winter. Consequently, knotweeds may reach maturity before leaving the survival stage. Moreover, we do not know if surviving their first winter truly means that young knotweeds will endure, especially for juveniles born from seeds or small fragments. Studies on survival should therefore last longer. Still, most regenerating ramets probably reach very quickly the incredibly high persistence that earned knotweeds their reputation (Pyšek *et al.*, 2001).

5.3. THE LOCAL SCALE

Soon after its birth, a knotweed will start its vegetative multiplication, quickly increasing its number of ramets. By doing so, the knotweed *individual* will become a *stand*, or more

precisely, a *clonal fragment* (Table 1). In open sites, clonal fragments will then quickly increase their size and resistance until becoming nearly impossible to eradicate. Over time, knotweeds will eventually fill the colonized sites thanks to three processes: clonal growth, local dispersal, and exogenous colonization (Pyšek & Hulme, 2005; Pauchard & Shea, 2006). If the first two are local processes, the latter depends on higher scale invasion dynamics (see section 5.4.). The *local scale* is the scale of population dynamics (Table 1). The *grain* and *extent* (cf. O'Neill *et al.*, 1986; Wiens, 1989) of the local scale range from a few square metre (i.e. the area that a nascent knotweed clonal fragment covers) to a few hectares (i.e. maximum foraging area of knotweed pollinating insects; Davis *et al.*, 2018), and local infilling by knotweeds may take only a few months or may last for centuries depending on local characteristics, especially propagule pressure and disturbance regime.

5.3.1. The clonal growth of knotweed stands

5.3.1.1. *Ontogeny and architecture of clonal fragments*

Despite its importance to understand their persistence and impacts, our knowledge of knotweeds' clonal growth and its ontogeny is incomplete. At some point of its development, a knotweed seedling or regenerating ramet will produce one or several plagiotropic rhizomes. These rhizomes will move away a short distance from their source and their apical meristem will give birth to new aerial shoots (Adachi *et al.*, 1996a). The new shoots will then produce adventitious roots and therefore become ramets (Table 1). The plant will also produce buds on most of its rhizome nodes and notably overwintering buds at the base of each shoot (Adachi *et al.*, 1996a; Martin *et al.*, in prep.). All the shoots will die due to frost in winter and basal nodes will give birth to new shoots in spring at almost the same location as the old ones, and so on every year. Over time, the basal area of each shoot will become highly lignified and form a large chunk of wood and buds called a shoot clump or a crown, that may be composed of one or several ramets (Adachi *et al.*, 1996a; Bailey *et al.*, 2009; Martin *et al.*, in prep.).

The growth of the rhizomatous system of knotweeds is sympodial. Adachi and colleagues (1996a) report that rhizomes axillary buds are maintained in dormancy due to the apical dominance of the nearest crown. And that only the deaths of crowns break dormancy, enabling rhizome branching from axillary buds. However, such observations may not be generalizable and the apical dominance of knotweeds in their introduced range and their branching patterns are likely affected by other factors (e.g. age of organs, obstacles, resource availability) as suggested by recent observations (Dauer & Jongejans, 2013; Martin *et al.*, in prep.). This is not trivial since branching patterns are important for the growth strategies of plants, and thus for the clonal mobility and lateral expansion of knotweeds (see below). When branching occurs, daughter rhizomes grow relatively rectilinearly if there are no obstacles (Figure 3). Some rhizomes may die or may wander without producing aerial shoots (and crowns), but many do. In the end, by repeating the sympodial development pattern presented above, knotweeds' clonal fragments grow (Smith *et al.*, 2007; Martin *et al.*, in prep.).

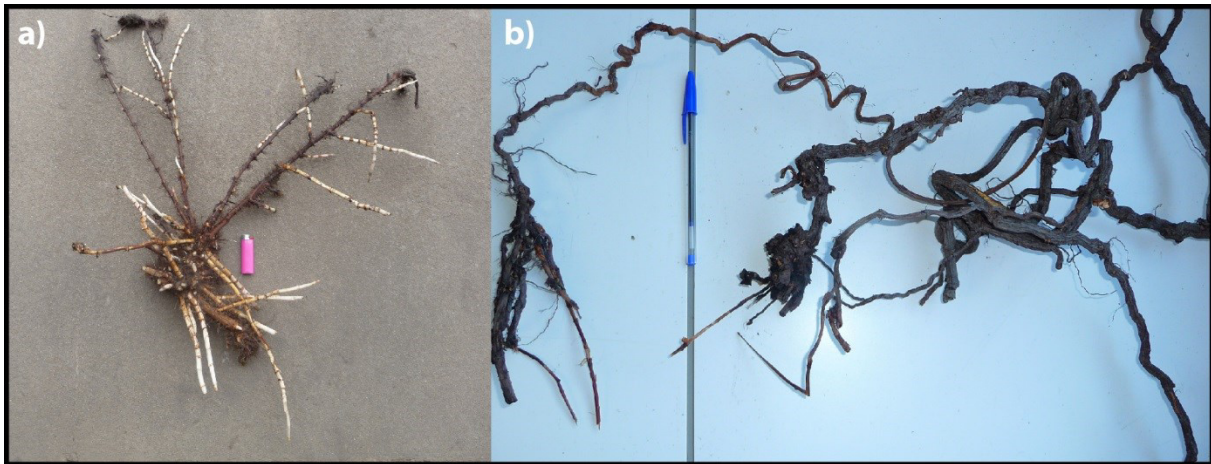


Figure 3. The various appearances of the rhizomatous networks of *R. japonica*. These organs came from a young plant that grew in a sandy-loam mixture (a), or from an older clone that grew in a semi-natural riparian soil (b).

5.3.1.2. Clonal growth strategies and knotweed expansion

Among the many assets that clonal plants possess, some are particularly important to understand the spatiotemporal dynamics of knotweeds. For instance, their ability to endlessly regenerate makes clonal plants virtually immortal (Harper & White, 1974; de Witte & Stöcklin, 2010). This persistence implies that the temporality of knotweed dynamics is potentially ill-suited to human observations. Some clonal plants are also able to share information and resources between ramets, a phenomenon known as *clonal integration* (Jónsdóttir & Watson, 1997; Stuefer *et al.*, 2004; Liu *et al.*, 2016). This capacity offers many advantages. Firstly, ramets growing in favourable habitat patches can sustain the growth of ramets growing in unfavourable patches. Secondly, clonal integration may enable clonal fragments to implement a *division of labour* between their constituting parts, with different ramets specializing in the acquisition of the locally most abundant resources, enhancing the overall performance of the clone (Alpert & Stuefer, 1997; Hutchings & Wijesinghe, 1997; Song *et al.*, 2013). Finally, integrated clonal fragments can adapt their future growth by sharing information on the growing conditions of local or distant ramets, potentially enabling them to adjust their foraging behaviour, select their habitat, or regulate inter-ramet competition (Jónsdóttir & Watson, 1997; de Kroon *et al.*, 2009; Liu *et al.*, 2016). It appears that *R. japonica* var. *compacta* performs clonal integration in order to support the growth of young ramets and avoid inter-ramet asymmetric competition (Suzuki, 1994a, b; Adachi *et al.*, 1996c). Yet, Price *et al.* (2002) found only little integration between ramets for *R. japonica*. This may be explained by age differences between the studied knotweeds (Price *et al.*, 2002), or by differences in their growing conditions: the Japanese studies examined plants in elevated nutrient-poor sites, while Price's knotweeds grew in quasi-optimal conditions. In nutrient-rich conditions, old ramets would have no need to support the growth of younger ones.

The expansion of knotweeds' clonal fragments is highly dependent on the environmental conditions that determine their growth strategies. As previously mentioned, in homogeneous yet nutrient-poor habitats such as the volcanic deserts of Japan, *R. japonica* var. *compacta*

adopts a growth form called *central die-back* (Adachi *et al.*, 1996a, b). There, knotweeds expand slowly in a centrifugal manner. With time, the central ramets of clonal fragments cease to produce shoots and give stands a ring-like appearance. To do so, clonal fragments produce more lateral buds on the outer-side of the clone, and keep a branching angle of 40° (Adachi *et al.*, 1996b). This enables maintaining a constant ramet density to maximize light interception while continuing expansion. This is a strategy of survival in unfertile environments, where the plant only uses space for a limited period of time (Adachi *et al.*, 1996a, b).

In knotweeds' introduced range, central die-back is seldom seen (but see Mummigatti, 2008; Pauková, 2013), possibly because knotweeds are usually dispersed on much richer soils. In undisturbed rich and sunny habitats, *R. japonica* adopts a *phalanx* growth form (Martin *et al.*, in prep.). This growth form is characterized by reduced rhizome length and increased branching frequency and thus, a high ramet density (Lovett Doust, 1981; Ye *et al.*, 2006). It is generally a space-consolidation strategy, with numerous tightly aggregated ramets to maximize resources exploitation and exclude other species (de Kroon & Schieving, 1990). To quickly perform space pre-emption, knotweed clones possibly have a high initial lateral expansion rate (lateral expansions of ca. 1.2 m-years⁻¹ have been observed for newly born clones)(Martin *et al.*, in prep.). With time, the lateral expansion rate of clones should get really slow (Herben & Hara, 1997; Thomas & Hay, 2004) as they get closer to an optimal size; i.e. that maximizes space occupancy and light interception while limiting the cost of an extensive rhizome network. This would explain why many knotweed stands in open-sites do not seem to expand much without disturbances (FM. Martin, pers. obs.): expanding too widely increases the chances of encountering unfavourable habitat patches, so space-consolidation may be a risk-avoidance strategy. To date, the largest confirmed clonal fragments covers a reasonable area of 65 m² (Masuzawa & Suzuki, 1991). Now, in shaded habitat, *R. japonica* appears to adopt a *guerilla* growth form (Martin *et al.*, in prep.), where plants produce longer rhizomes with fewer branches and ramets (Lovett Doust, 1981; Ye *et al.*, 2006). The clones then can exhibit either a foraging strategy (with a few long rhizomes that “search” the habitat to selectively place ramets in more favourable patches), or a conservative strategy (where clonal proliferation is restricted due to resource limitation)(Lovett Doust, 1981; de Kroon & Schieving, 1990; Herben & Hara, 1997). Foraging guerilla clones usually expand faster than phalanx clones (Stuefer, 1996; Herben & Hara, 1997), but conservative clones certainly do not expand much.

Many invaded sites have more complex environmental conditions than those mentioned above (e.g. heterogeneity in soil humidity, nutrient levels, disturbances, distribution of obstacles), likely leading to modifications of growth strategies and lateral expansion rates. Smith and colleagues (2007), on a *R. japonica* stand growing on backfill alongside a road and a forest, found that rhizome length and branching angles was much more variable than what was found by Adachi's team. Their model assumed that clonal fragments expand quadratically with time (Smith *et al.*, 2007). Yet, to date, no empirical evidence supports this hypothesis. To our knowledge, no field study ever measured the expansion rate of *clonal fragments* (Martin *et al.*, in prep.), and the very few that measured the one of *stands* (see Section 5.3.2.2.) used only two dates and showed that expansion was highly variable (e.g. Alberternst & Böhmer, 2006; Pauková, 2013; Martin *et al.*, 2019). Some authors also report that wandering rhizomes may

be found up to 7m (Child & Wade, 2000) or even 15-20m (Fuchs, 1957) beyond the aboveground limits of stands. Such observations are interesting as they may be evidence of an escape-strategy or of habitat exploration. Nevertheless, this behaviour may be unusual since recent data showed that in average, rhizomes are not found further than 1 or 2m away from stands (Fennell *et al.*, 2018). On the other hand, the same authors confirmed that knotweed rhizomes can grow deep (down to 3m), but as they observed that rhizomes prefer to circumvent obstacles rather than go through them (Fennell *et al.*, 2018), obstacle avoidance may be the cause of such deep rhizome occurrences. A key driver that may alter the clonal growth and expansion rates of knotweeds' clonal fragments is disturbances, notably by mowing/cutting. Mowing possibly promotes the lateral expansion of clonal fragments (Beerling, 1990), likely by suppressing apical dominance and thus favouring rhizome branching. Conversely, repeated destruction of aerial shoots should deplete rhizomes and favour, *in fine*, a regression of clonal fragments. However, empirical and modelling data suggest that the aerial parts of knotweeds should be *entirely* destroyed at least 4-6 times a year to hope seeing an effect on their spatial coverage and/or dynamics (Seiger & Merchant, 1997; Gerber *et al.*, 2010; Martin *et al.*, in prep.). Finally, the chemical properties of soils and their heterogeneity may affect the spatiotemporal dynamics of clonal fragments. For instance, pollution by metals may promote the clonal growth of knotweeds (Michalet *et al.*, 2017), and their allelochemicals may enable them to build their own environmental niche and thus favour their own expansion (e.g. Dassonville *et al.*, 2011; Parepa *et al.*, 2013; Bardon *et al.*, 2014).

5.3.2. Site infilling and knotweed spread

5.3.2.1. *The sexual reproduction and genetic structure of knotweeds*

Due to its importance for natural selection, evolution and invasion dynamics, the sexual reproduction of knotweeds is an important local process even though highly site-specific. Knotweeds are gynodioecious (or subdioecious), i.e. there are hermaphrodite (male-fertile) and female (male-sterile) individuals (Hollingsworth *et al.*, 1999; Bailey *et al.*, 2009), meaning that, except in the rare occasions of auto-incompatibility failure (Bailey, 1994), sexual reproduction on a given site requires the presence of both sexes in the population. This, in turn, depends on higher scale processes, such as the regional dynamics of individuals of each sexes or even the continental history of introduction of each sexes (e.g. there will be no *R. japonica* seedlings in Australia if both sexes have not been introduced). On the other hand, knotweeds possess huge hybridization abilities (Bailey *et al.*, 2007; Tiébré *et al.*, 2007b), so the two gamete providers may well belong to different taxa. Actually, all invasive knotweed species can breed between each other (Bailey *et al.*, 2007; Saad *et al.*, 2011), and they may even hybridize with other *Polygonaceae* species with differing life forms such as woody climbers (*Fallopia baldschuanica*) or lianas (*Muehlenbeckia australis*)(Bailey, 2013). Nevertheless, the genetic structure and the subsequent success and dynamics of the progeny of any plant species depend on the characteristics of the potential parents (Hutchings, 1996), so the quality of the progeny will vary with the identity of the parents (e.g. taxa, ploidy level).

Technically, knotweed fruits are winged achenes (samaras), harbouring by definition only one seed per achene.

The knotweeds of the section *Reynoutria* have a chromosome base number of 11. However, due to their inclination towards hybridization, backcrossing and polyploidization, knotweeds can display an impressive array of ploidy levels (from $2n = 32$ to 154) (Kim & Park, 2000; Bailey, 2001, 2003; Bailey *et al.*, 2007, 2009; Gammon *et al.*, 2010; Bailey, 2013; Hoste *et al.*, 2017; Park *et al.*, 2018). Of course, some are more common than others, but almost all combinations (even the hybrids) can be potentially fertile and thus act as parent (Pashley *et al.*, 2003; Tiébré *et al.*, 2007a; Tiébré *et al.*, 2007b). Still, often, only a small fraction of flowers are fertilized, indicating a lack of nearby pollen donors (Bailey, 1994). The pollination of knotweeds is exclusively entomophilous (Kawano *et al.*, 1999; Barney *et al.*, 2006). In their introduced range, it seems that pollinating insects took a few decades to get accustomed to knotweeds (Beerling *et al.*, 1994), but now they are frequently visited by a wide range of insects (Davis *et al.*, 2018). However, despite their importance for the genetic structure of populations, we know almost nothing about the spatial dynamics of knotweed pollinators (but see Zhou *et al.*, 2003).

Depending on the composition of populations (in terms of taxa, sexes and ploidy levels), a site will have a low or high potential for sexual reproduction. Some sites may be considered as evolutionary hotspots (Pashley *et al.*, 2003; Tiébré *et al.*, 2007b; Berchová-Bímová *et al.*, in prep.), notably if *R. japonica* and male-fertile *R. sachalinensis* are both present (or the fertile hybrids). Such sites may favour the selection of more adapted genotypes (Mandák *et al.*, 2005; Bailey *et al.*, 2007; Gillies *et al.*, 2016; Rouifed *et al.*, 2018b; Berchová-Bímová *et al.*, in prep.) and, consequently, have an important impact in further regional invasion dynamics by becoming a potential source of higher quality propagules. To produce such seeds, knotweeds additionally need warm summers and frostless autumns (Bailey, 1994; Beerling *et al.*, 1994). Besides that, provided sufficient pollination, they have a huge fructification potential. A single knotweed stem can bear more than 100.000 flowers, meaning that a knotweed stand can potentially produce millions of seeds annually (Bram & McNair, 2004).

5.3.2.2. *Knotweed stands expansion and short distance dispersal*

With time, any suitable site colonized by knotweeds should be infilled by them. The actual time-scale of such infilling now depends on the site location and landscape context, its colonization history (e.g. single or repeated introduction, type of taxa and sexes introduced), and especially its disturbance regime.

In undisturbed sites away from dynamic rivers, local spread of knotweeds should be extremely slow. If a site is colonized by a single isolated clonal fragment, this one should not expand much and will certainly have a very limited and localized impact on native species. For knotweed populations (several individuals), even if sexual reproduction occurs, local infilling will likely take centuries because there would be very few opportunities for the dispersal of vegetative propagules and the establishment of seedlings without disturbances (see section 5.2.2.). This is even more likely when we know that most knotweed achenes fall just beneath their mother, wind dispersal beyond a few metres being rare (Zhou *et al.*, 2003; Tiébré *et al.*,

2007b). In such places, the infilling would be mainly performed through the vegetative expansion of clonal fragments and *stands* (Table 1). Stands, which may be composed of many aggregated clonal fragments, likely expand differently than clonal fragments, but we do not know much about this difference. Recent work suggests that stands expand with time, possibly more quickly at first to ensure spatial pre-emption (Martin *et al.*, 2019). But the impossibility to distinguish *in situ* clonal fragments from stands impedes our ability to draw conclusions from observed patterns. Since intraspecific competition is usually symmetrical between clones, close proximity between them could also promote their spatial expansion (avoidance) rather than their exclusion (de Kroon *et al.*, 1992); i.e. clones would display faster lateral growth on the sides that are free of competition. But this remains to be tested. To our knowledge, the only study that undoubtedly examined stands (and not clonal fragments) focused on the effect of ecological restoration on knotweed performances and proliferation (Dommanget *et al.*, 2019). It showed that, without competition, the ramets of young *R. japonica* stands progressed of 2 metres in average in 2 years, with rhizomes growing even further. It also showed that dense plantations of *Salix viminalis* reduced by half this expansion, and that competition significantly reduced ramet density and biomass production (Dommanget *et al.*, 2019).

In disturbed habitats, knotweeds' infilling dynamics are much quicker but depend on the type, frequency and intensity of disturbances. Disturbances can indeed favour the fragmentation and dispersal of knotweed tissues, of achenes, and open windows of opportunity for their establishment. One of the most common sources of disturbance around knotweed stands is the management applied to control their spread. Instead of limiting their spread, mechanical techniques such as mowing, flailing or shredding seem to have no effects or positive ones on stands expansion, especially when applied at low frequency (Beerling & Palmer, 1994; Child & Wade, 2000; Barney, 2006; Delbart *et al.*, 2012; Monty *et al.*, 2015; Schifflerthner & Essl, 2016; Martin *et al.*, 2019). This is even truer if the management does not cover the entirety of stands (Martin *et al.*, 2019; Martin *et al.*, in prep.). On the other hand, using measures on 574 knotweed stands, Breton and colleagues (in prep.) showed that stands tend to be smaller when they are mowed at least 3 times a year. As most of these stands were located at the very edge of *transportation corridors* (roads, railways, and navigable rivers), it is possible that they experienced mowing from their establishment onward, as part of the regular maintenance of these infrastructure's edges. Such early and repeated mowing would have then prevented stands to acquire too much reserve, and reduced the probability of survival of the dispersed stem fragments. Furthermore, expansion may have been impeded by the linear obstacles represented by these transportation corridors (e.g. Martin *et al.*, 2019). Other anthropic activities are known to act as short-distance dispersal vectors for knotweeds propagules, such as snow removal (Ducey & O'Brien, 2010) or earth movement (Beerling, 1991; Beerling & Palmer, 1994; Dawson & Holland, 1999; Child & Wade, 2000; Shaw & Seiger, 2002). Additionally, anthropic activities may import new knotweed propagules from exogenous sources to take part in local infilling.

Natural disturbances can also disperse and spread knotweeds. Although never reported, rock-falls and debris flows could theoretically act as downward dispersal vectors in mountains valleys. Unsurprisingly, rivers are the most reported natural dispersal vectors for

knotweeds. Regular river flow may transport and drop achenes off along river banks, and floods can spread propagules downstream and create establishment opportunities (Beerling *et al.*, 1994; Pyšek & Prach, 1994; Dawson & Holland, 1999; Pashley *et al.*, 2003; Barney, 2006; Colleran & Goodall, 2014; Lamberti-Raverot *et al.*, 2017). Nonetheless, we know almost nothing on the dynamics and patterns of short-distance dispersal by rivers and of the interplay between knotweeds demography, river characteristics, and larger scale hydrogeomorphological dynamics (see section 5.4.1.2.). Some data suggest that local water dispersal might be the rule rather than the exception, at least for streams and small rivers (Duquette *et al.*, 2015; Barthod & Boyer, 2019): in 2018, along 104 km of hydrographic network, 85% of the new juveniles found in riparian habitats ($n = 340$) were located less than 100 metres away from the nearest knotweed stand, and only 5% were found further than 500 metres away (Barthod & Boyer, 2019). Still, it may be different for other river-systems or in the case of major floods. Important research efforts are needed to improve our knowledge on those processes. Other factors may furthermore affect riparian dynamics: e.g. coypus (*Myocastor coypus*) and other rodents have been seen favouring knotweed's fragmentation and dispersal by destabilising invaded riverbanks (O. Forestier, pers. comm.), cutting stems (Barthod & Boyer, 2019), or decreasing the competitive pressure on knotweeds by eating native riparian willows (Dommaget *et al.*, 2015). Whatever the dispersal process involved, such riparian spread may cause semi-continuous colonization over kilometres (Figure 4).



Figure 4. The colours of autumn sometimes reveal the degree of invasion of some habitats (photo credits: FM. Martin, 2017).

Locally, the fusion of knotweed stands may be a process of importance for the understanding of their long-term spatial patterns and their impacts on native species. To date, no works exist on this topic, but it could be a good application for remote sensing techniques (e.g. Müllerová *et al.*, 2017; Martin *et al.*, 2018).

It appears then that disturbances are a key factor for the temporal and spatial dimensions of local invasion dynamics by knotweeds. They can strongly speed-up the spread of these plants, and might be the main drivers creating the thousands-of-square-metres-large stands that exist in some populations. In turn, these local populations may become important for larger-scale dynamics, notably due to their enormous propagule bank. Some authors indeed estimate that there can be 90 stem-propagules m^{-2} (de Waal, 2001) and at least 238 rhizome-propagules m^{-2} (Brock & Wade, 1992) in addition to the millions of seeds that may be produced annually by knotweed stands (see section 5.3.2.1.).

5.4. THE REGIONAL SCALE

The spread of INPSs such as knotweeds is not restricted to short-distance dispersal. Actually, for many plants, spread involves simultaneously local expansion dynamics and long-distance dispersal (Collingham *et al.*, 2000; Pyšek & Hulme, 2005; Pauchard & Shea, 2006), a mechanism sometimes referred to as *stratified diffusion* (Shigesada *et al.*, 1995; Higgins & Richardson, 1999). Beyond a certain distance, juveniles established from dispersed propagules will be too distant to maintain direct interactions (e.g. sexual reproduction) with their parental population. We therefore consider that such distant knotweeds form or join other populations distinct from the parental ones (Table 1). The ensemble of all populations connected through long-distance dispersal (LDD) in a landscape is here referred to as a *metapopulation* (Table 1). The regional scale is the scale of metapopulation dynamics: i.e. the regional spread of knotweeds through LDD, and the subsequent *potential range filling* that ensues over time.

The spatial *grain* (cf. O'Neill *et al.*, 1986; Wiens, 1989) of the regional scale represents knotweed populations, while the *extent* of this scale may cover thousands of square kilometres as it includes the vast areas over which dispersal vectors may transport the propagules of the regional populations (e.g. the hydrographic network of a watershed; a basin of anthropic activities).

Regional spread is characterized by a high temporal variability (Williamson *et al.*, 2003; Pyšek & Hulme, 2005) that stems from regional differences in invasion history, landscape and population characteristics, and disturbance regime (With, 2002; Hastings *et al.*, 2005; Theoharides & Dukes, 2007). In turn, these differences will have consequences on a corollary of metapopulation dynamics' investigations: regional prediction modelling.

5.4.1. Landscape patterns and metapopulation dynamics

The long-distance dispersal (LDD) of plants is a complex and versatile phenomenon (Nathan, 2006). For knotweeds, LDD is mainly the doing of water and humans (Pyšek & Prach, 1993; Beerling *et al.*, 1994; Barney *et al.*, 2006).

5.4.1.1. *Knotweeds potential for hydrochory*

Observations of sea dispersal (Bailey, 1994) and lake dispersal (Barthod & Boyer, 2019) of knotweed propagules exist. Still, water LDD is by far the doing of rivers. All the propagule types of knotweeds may be transported by rivers.

Achenes of *R. x bohemica* can float between 2 and 5 days in agitated water with seeds remaining highly viable (Rouified *et al.*, 2011; Lamberti-Raverot *et al.*, 2017; Lamberti-Raverot *et al.*, 2019). In experimental settings, seeds may even germinate in the water (with a water around 20°C), thus increasing the time of buoyancy up to 20 more days (Rouified *et al.*, 2011; Lamberti-Raverot *et al.*, 2019). In the wild however, achenes are ready to be dispersed at the end of autumn, such germination would thus likely be prevented (or highly limited) by cold water temperatures. Still, achenes' buoyancy theoretically enables dispersion over long distances: a floating duration of 40h in a river with a surface velocity of 62.5 cm·s⁻¹ could transport achenes over 90 km (Rendu *et al.*, 2017). But many factors may affect such distance of dispersal: e.g. obstacles, physicochemical properties of water, variations in river morphometry (Lamberti-Raverot *et al.*, 2017; Rendu *et al.*, 2017). Although seedling establishment is rare, several authors report successful LDD and establishment of hybrid knotweeds in the wild (Hart *et al.*, 1997; Tiébré *et al.*, 2008; Gaskin *et al.*, 2014). Interestingly, variations between riparian populations in the morphological traits important for the floatability of hybrid achenes have been observed (Lamberti-Raverot *et al.*, 2017; Lamberti-Raverot *et al.*, 2019), suggesting that selection for more adapted genotypes may be occurring. Yet, more research is needed to confirm this hypothesis. It would also be important to know if the other knotweed taxa present similar floatability capacities.

Laboratory experiments showed that *R. x bohemica* stem fragments can also float and remain viable in water for several days (some may even stay afloat for 2 months), while rhizome fragments sink but stay viable for at least a month in water (Lamberti-Raverot, 2016; Puijalon *et al.*, 2019). Stem floatability mainly depends on its morphology, particularly on the proportion of hollow tissues in the internodes that may vary depending on its genotype and growing conditions, and so does rhizome viability (Lamberti-Raverot, 2016). Still, we know nothing of stems' floatability in actual rivers, the differences with the other knotweed taxa, and of the distances these clonal propagules are truly capable to cross.

5.4.1.2. *Hydrogeomorphology, riparian landscapes and long-distance dispersal*

Being able to float on water or endure submersion for a long time gives no indication on the frequency of LDD events, the actual shape of the dispersal curves (Figure 5), or the rate of spread of a given watershed. This information will depend on the localization and characteristics of knotweed populations, the landscape context, and the hydrogeomorphological dynamics. And all this would of course evolve through time. Although very few data exist on this topic, several hypotheses can be formulated (representing as many research questions):

- Seasonal differences in the contribution of the various types of propagules to river dispersal must exist (Lamberti-Raverot, 2016; Puijalon *et al.*, 2019): rhizomes can likely

be spread all year long, but seeds dispersed in late summer or early autumn would not be viable (see section 5.2.1.1.), and stem fragments would have a declining probability of regeneration from mid-summer onward due to translocation of reserves and shorter growth-time before winter.

- Semi-natural riverbanks and alluvial forests will have a slower rate of spread than open and artificialized riparian habitats (Navratil *et al.*, 2018) thanks to lower invasibility.
- Rhizome dispersal only occurs when riverbanks are eroded. Erosion is mostly the deed of floods but can also arise from boat-waves, animals, anthropic activities, or scouring by floating ice (e.g. Duquette *et al.*, 2015).
- Even if they do not float, rhizomes are by far the first contributors to the regional expansion along rivers. Studies report that rhizomes or juveniles born from rhizomes represent 70-95% of the knotweeds found in riparian areas after a flood, the rest coming from stems (Colleran & Goodall, 2014; Barthod & Boyer, 2019). This contribution should also increase with increasing sedimentation during floods, as rhizome fragments have a much higher probability of regeneration with important burial depth (Francis *et al.*, 2008).
- Along un-channelized rivers, the rate of spread should be proportional to its hydrogeomorphological dynamism (that is mainly related to its slope and thus, flow velocity)(Dawson & Holland, 1999; Ness *et al.*, 2008; Barthod & Boyer, 2019). A dynamic river will be invaded more rapidly than a less dynamic one, for an initially comparable degree of invasion and riparian vegetation integrity. Even during a flood, a slow flow velocity should limit the number of dispersed propagules, their dispersal distance, and their establishment opportunities. This may explain why some large European plain rivers appear to slow invasion dynamics (Schnitzler & Müller, 1998; Bailey & Schnitzler, 2003; Bailey & Wisskirchen, 2006; Navratil *et al.*, 2018).
- Violent floods may lead to very quick spread. For instance, Barthod & Boyer (2019) report that along 23 km of the Hérault river (Mediterranean France), two major floods in 9 years led to an increase in invaded surfaces of about 43 times (from 91 stands covering 500 m² to 611 covering 21.500 m²) and an advance of the colonization front of 14 km. Along the Séveraise river (French Alps), a few discrete stands existed since 1930 when a summer flood in 2008 spread knotweeds over 17 km, creating 200 new stands (ARRA, 2010).
- Along unrectified river sections, there should be more knotweeds in the sedimentation zones of riverbanks than on the erosion zones, at least in the short-term. This would however change more or less quickly with channel mobility.
- The rate of spread should increase with the residence time of riparian knotweeds along the river (van Oorschot *et al.*, 2017), at least until the river colonization reaches a plateau.

As the spread occurs, regional patterns of taxonomic and/or genetic diversity may appear depending on the dispersed propagules, and on the composition and ploidy levels of the parental populations (Gaskin *et al.*, 2014; Lamberti-Raverot *et al.*, 2017). Examples of such patterns may be found near Québec (Duquette *et al.*, 2015), Glasgow (Hart *et al.*, 1997), in Slovenia (Zelnik *et al.*, 2015) and in north Bohemia (Bímová *et al.*, 2004). Still, the lack of data makes generalizations difficult to ascertain. Moreover, the expansion dynamics of riparian knotweeds and the patterns they create may be complicated by anthropogenic LDD events.

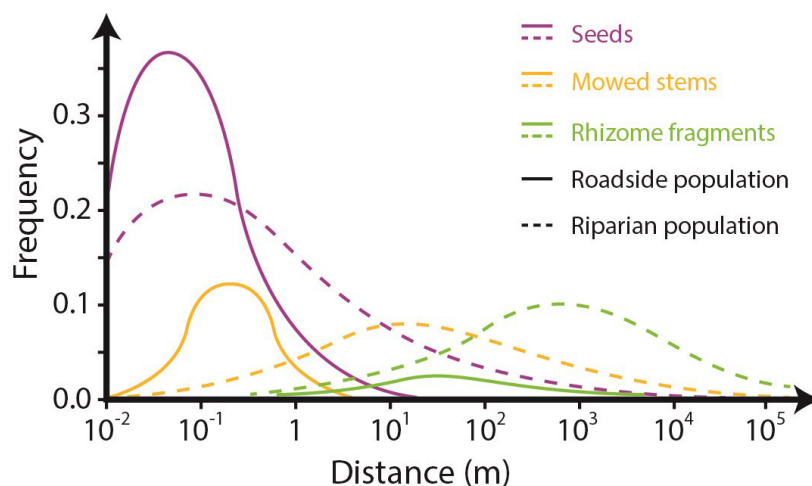


Figure 5. Hypothetical dispersal curves for various propagule types from two different possible populations: a roadside population (plain lines) and a riparian population (dashed lines). The shape of all these curves is defensible yet they may all be wrong, and no simple dispersal function could likely approximate them all. In fact, we ignore the true shape of many demographic functions (e.g. population growth rate) or responses (cf. Austin, 2007; de Witte & Stöcklin, 2010; Gurevitch *et al.*, 2016).

5.4.1.3. *The role of anthropogenic knotweed spread*

In addition to introducing knotweeds and frequently spreading them locally, anthropic activities are often responsible for LDD events. Anthropogenic-LDD is a special kind of spread as it enables propagules to quickly move across dispersal barriers that would otherwise prevent or slow considerably further spread down. Although widely acknowledged as important and often unintentional (Pyšek & Prach, 1993; Beerling *et al.*, 1994; Shaw & Seiger, 2002; Barney, 2006), almost no quantitative data exist on this type of dispersal.

The two main ways of anthropogenic-LDD are through the movement of earth or construction machines contaminated with propagules, and through green-waste disposal. In some areas, these vectors appear to be the main source of knotweed expansion (Pyšek & Prach, 1993; Beerling & Palmer, 1994; Barney, 2006; Rouifed *et al.*, 2014). Actually, anthropogenic expansion is likely the main cause of the majority of non-riparian knotweed populations. The repeated occurrences of the same genotypes across a region give evidences of such dispersal. For instance, the same hybrid genotype was found in 13 different populations across the states of Idaho, Montana, Oregon, Washington and Wyoming in the USA (Gaskin *et al.*, 2014).

The frequency and the distance of anthropogenic-LDD are hard to assess. In Czech Republic, it appears that more than 2/3 of the new knotweed populations are located in non-riparian areas (Pyšek & Prach, 1993), emphasizing the paramount importance of anthropogenic dispersal for knotweeds' range expansion. In the UK, Hulme (2003) showed that the median distance between newly invaded sites in 1920 and the nearest known populations of *R. japonica* in 1900 was 30 km, and that distances longer than 100 km were not uncommon. If we assume the parenthood of these already known populations over the new ones of 1920, then it gives a probability of LDD over 20 km of 0.5 per year (Hulme, 2003).

Although very enlightening, this estimation must be considered with caution. Firstly, a substantial part of the propagules responsible for these colonization events may come from other populations than the nearest ones, or may have been dispersed by rivers. Secondly, estimates based on these old data from the UK may not be representative of the current situation in the same region, or in other parts of the world. For instance, there must be a relationship between the regional probability of anthropogenic spread and human-population density and economic activities, as suggested from expansion data from the British Isles and Czech Republic (Williamson *et al.*, 2003; Williamson *et al.*, 2005). We may also assume that the likelihood of anthropogenic LDD varies with the *minimum residence time* (cf. Richardson & Pyšek, 2006) and the level of public awareness (especially public-works professionals), two drivers that have changed since 1920. Incidentally, regional differences may exist in the perception of knotweeds (e.g. Palmer, 1994; Cottet *et al.*, 2015; Rouifed *et al.*, 2018a) and therefore in the effects of this perception on control measures and spread. For instance, anthropic interactions with knotweeds certainly differ between Japan, where these plants are regarded as familiar and useful (Shimoda & Yamasaki, 2016), Great-Britain, where knotweeds are regarded as pests and are subject to regular media coverage (Shaw, 2014; Robinson *et al.*, 2017a; Robinson *et al.*, 2017b), and France, where knotweeds are quite unknown from the general public (Rouifed *et al.*, 2018a). Consequently, generalizations are hard to make.

5.4.1.4. *Quantifying the rate of spread and understanding regional expansion*

At the regional scale, spread is composed of LDD events but also of local dispersal and infilling. As discussed in the previous sections, it is hard to obtain data on the growth rate of knotweed populations, as well as on the frequency and distance of dispersal events (*natural* or anthropogenic). Getting a single measurement that encompasses the numerous aspects of the spread of knotweeds (or any INPS) is therefore extremely difficult (Pyšek & Hulme, 2005), and spread may be expressed in various metrics related to distance or to surfaces (Pyšek & Hulme, 2005; Williamson *et al.*, 2005). Yet, a good estimate of the rate of spread of knotweeds is essential to predict the continuation of the invasion and to act accordingly.

To acquire very accurate data on the regional expansion of an INPS, repeated field campaigns or remote sensing are likely the best options (Hastings *et al.*, 2005; Huang & Asner, 2009). Nonetheless, repeated field campaigns over large extent are extremely time-consuming and the remote identification of plants requires the development of species-specific methods. Regarding knotweeds, operational methods for semi-automated remote detection (through satellite imagery or aerial orthophotos) were unavailable until very recently (Müllerová *et al.*, 2017; Martin *et al.*, 2018). Alternatively, records from herbaria, species lists or weed inventories from protected areas and regional authorities may be used to follow the sequential colonization of space-units across a landscape (Hastings *et al.*, 2005; Pyšek & Hulme, 2005).

Even if data are available, giving a quantitative estimation of the regional spread of knotweeds (or any other INPS) presents several issues and shortcomings that one should be aware of:

- Knotweeds expansion rate is not constant over space and time, as suggested by evidences from cumulative number of colonized spatial-units (e.g. localities, quadrats, counties, states), highlighting important differences between regions. In England and Wales, *R. japonica*'s spread displayed three distinct phases of expansion (*logistic curve*): a slow increase in occupancy from initial introductions to the 1940's, followed by an exponential phase of expansion and a deceleration from the 1960's onward (Figure 6a)(Hulme, 2003; Pyšek & Hulme, 2005). Approximately the same pattern was found in Ireland with slightly different dates, but without the asymptotic phase (Figure 6b)(Pyšek & Hulme, 2005). In Czech Republic however, Williamson *et al.* (2005) report that *R. japonica*'s expansion only displayed a short exponential phase (between 1892 and 1911) with a simultaneous quadratic increase that lasted until the last records in 1995, while *R. sachalinensis* was only recorded between 1951 and 1995 and increased only quadratically (Figure 6b). These differences certainly represent different stages of invasion. Any metric of spread would thus differ according to the period and region investigated (see below).

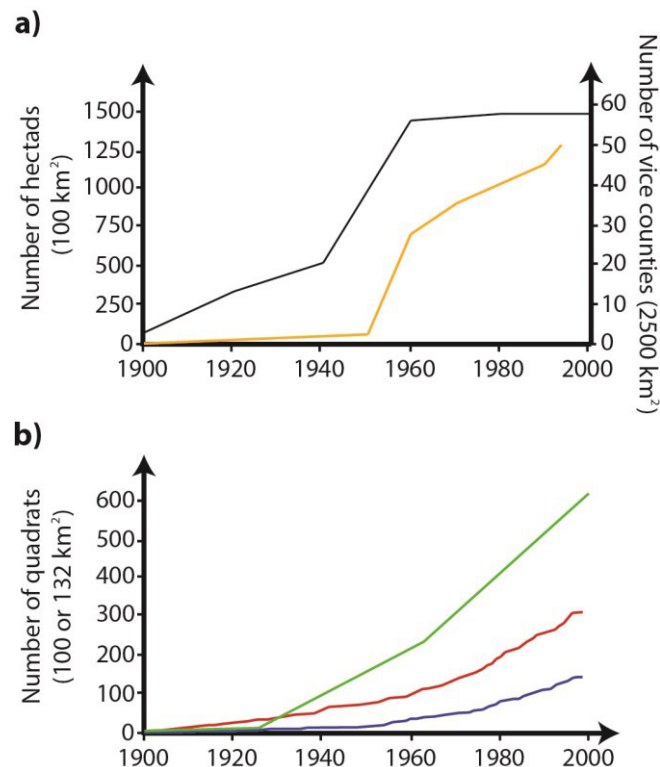


Figure 6. The rate of spread of (a) *R. japonica* in England and Wales as measured by the cumulative number of colonized hectads (10 x 10 km; yellow line), or the cumulative number of colonized vice-counties (black line); and (b) of *R. japonica* in Ireland (green line) and Czech Republic (red line) or *R. sachalinensis* in Czech Republic (blue line) as measured by the cumulative number of quadrats (10 x 10 km for Ireland, and 11 x 12 km for Czech Republic). Redrawn and modified from Pyšek & Hulme (2005) with permission from the authors (the Czech data are a courtesy of Petr Pyšek).

- Estimates of spread are also strongly influenced by the spatial and temporal resolution of the data they are estimated from (Collingham *et al.*, 2000; Hastings *et al.*, 2005; Pyšek & Hulme, 2005). This may lead to inconsistent and/or incomparable results. In

Figure 6a for instance, knotweed spread appears to be much faster and more dramatic when captured by the number of invaded vice-counties than by the number of colonized hectads (for which an apparent lag-phase occurs). Coarse resolution data indeed overestimate both the rate of spread and the colonized area (Hulme, 2003), possibly because they represent more faithfully LDD events and new introductions than the short-distance expansion that happen simultaneously (Pyšek & Hulme, 2005). Other examples exist. In Czech Republic, using the number of invaded localities instead of quadrats, some authors have found expansion curves characterized by lag-phases followed by exponential growth (Pyšek & Prach, 1993; Mandák *et al.*, 2004), while others did not (Williamson *et al.*, 2005). For North America, Barney (2006) reported that *R. japonica*'s expansion curve displayed the typical logistic shape, yet with strong differences between Canada and the USA. However, his data was based on the incremental colonization of *political units* (US counties and Canadian municipalities) that covered a wide range of spatial scales preventing comparisons to be made with other datasets: e.g. one of the invaded Canadian units, the Thunder Bay district, covers an area larger than Ireland or Czech Republic. This resolution problem for North American data had already been highlighted by Hulme (2003).

- Similar demonstration may be used to underline the role of temporal resolution. In England and Wales, *R. japonica*'s mean annual rate of increase is 15% when computed using decadal surveys, 36% for 50-years records, and 295% if only the first and last records are used (Pyšek & Hulme, 2005). To be relevant and comparable, rates of spread at a given scale should therefore be calculated on data with similar spatial and temporal resolutions, during a similar phase of expansion (i.e. lag, exponential or asymptotic): e.g. in the last decades, at comparable resolution (ca. 100 km²), *R. japonica* and *R. sachalinensis* had rates of spread of 4.3 and 2 km·y⁻¹ in the UK, respectively (Williamson *et al.*, 2003), and 2.07 and 2.27 km·y⁻¹ in Czech Republic (Williamson *et al.*, 2005).
- Data from herbaria or species lists are not exhaustive and present spatial sampling biases (Mandák *et al.*, 2004; Barney, 2006): e.g. public and accessible lands have more chances to be sampled than private or secluded ones, plants easily identifiable may be more sampled than complicated ones (such as *R. x bohemica*). Moreover, knotweeds are famously difficult to distinguish, and confusion between taxa may further alter the quality of the records (cf. Mandák *et al.*, 2004; Meerts & Tiébré, 2007; Vuković *et al.*, 2019).
- At any given stage of invasion (from establishment to LDD and regional spread), stochastic events occur (e.g. floods, storms, nutrient pulses, anthropogenic transport or disturbances) that may facilitate the success of plants like knotweeds (Murphy & Lovett-Doust, 2004; Pyšek & Hulme, 2005; Tiébré *et al.*, 2008). This shortcoming is difficult to account for.

Beyond pure methodological considerations, understanding the source of regional differences in expansion patterns is important to improve and interpret predictions. As discussed above, the regional spread of knotweeds may be chopped in several phases whose

presence/absence and timing may have various explications. On the one hand, it may be an artefact related to the coarse resolution of the data. New introductions at larger scale may somehow artificially increase the actual expansion rate of local populations whose spread may experience a lag. On the other hand, the impression of lag may be due to LDD that the data could not capture (Pyšek & Hulme, 2005). We may also falsely infer a regional saturation while the regional infilling is still extremely dynamic (Figure 6). If a true lag exists, a lack of genetic diversity and local adaptation may possibly play a role (Crooks, 2005; Lockwood *et al.*, 2013), mostly for hybrid knotweeds, but the most likely explanation resides in the isolation of populations. The lag may represent the time needed for populations, to reach (or be reached by) key dispersal vectors (Pyšek & Prach, 1993; Pyšek & Hulme, 2005). Most initial knotweed introductions have been in gardens (Conolly, 1977; Bailey & Conolly, 2000; Del Tredici, 2017) and, as without disturbances the local dynamics of knotweeds are often extremely slow (see section 5.3.2.), escaped populations (or newly introduced ones) may have taken decades to spread enough to find vectors of multidirectional LDD and thus trigger range expansion. In fine, the duration of lag-phases and the subsequent beginning of exponential ones may be mainly explained by the density of anthropic populations and activities (Pyšek & Hulme, 2005; Williamson *et al.*, 2005; Pyšek *et al.*, 2010), the residence time of knotweeds (e.g. Beerling & Palmer, 1994), and the number and geography of introductions. It would furthermore explain why, regardless of the region, most exponential phases began around World War II; i.e. a period that experienced a strong rise in human population and economic activities, notably in constructions (paramount for knotweed dispersal).

Exponential, quadratic and asymptotic phases are more straightforward to understand. Important range expansions, whether exponential or quadratic, are governed by the frequency of anthropogenic LDD and, to a lesser extent, of *natural* LDD (Pyšek & Hulme, 2005; Theoharides & Dukes, 2007). More precisely, the slopes of expansion curves depend on the proportion of LDD compared to the short-distance dispersal events of populations (Shigesada *et al.*, 1995).

Subsequent deceleration (asymptotic phase) may possibly stem from a true saturation; i.e. colonization of most suitable habitat patches, but this eventuality must be extremely rare for knotweeds. Firstly, because of the vastness of the range of most metapopulations. Secondly, because the concept of *favourable habitat* is ambiguous for most plants (Freckleton & Watkinson, 2002; Murphy & Lovett-Doust, 2004), and knotweeds may perhaps be considered as *Jack-and-Master* species (cf. Richards *et al.*, 2006) that possess such wide fundamental niche and environmental tolerance that they may colonize most terrestrial temperate habitats (see section 5.4.2.). More often, apparent decelerating rates of spread may either be due to resolution artefacts (see above), or decreasing frequency of LDD events. Several drivers may cause such decrease: e.g. changes in the regional economic or demographic situation, changes in the hydrogeomorphological dynamics, ban on knotweed trade (cf. Mandák *et al.*, 2004; Barney, 2006), increasing public awareness.

Landscape patterns and patterns in the metapopulation itself may also play a role in the regional spread of knotweeds. Urban or suburban areas, the density of the road and hydrographic networks, meso-topography, and the proportion of *less favourable* habitat patches (e.g. dry soils, closed-forests) may influence range expansion and its directionality.

Urban heat island may also increase the probability of seedling establishment (Groeneveld *et al.*, 2014) and thus favour the spread and genetic diversity of the local populations. Moreover, the taxonomic composition (and ploidy levels) of the regional knotweed populations may also affect the metapopulation dynamics as several authors suggest that *R. x bohemica* spread faster than its parental species (Pyšek *et al.*, 2003; Mandák *et al.*, 2004; Vuković *et al.*, 2019), although it was not always found (Tiébré *et al.*, 2008). The distribution and the size of populations may also act on range expansion. It appears that the rate of spread is higher when the expansion is made from numerous small foci than a few large populations (Pyšek & Hulme, 2005). Finally, landscape heterogeneity is known to affect the rate of spread of INPSs (Keitt *et al.*, 2001; With, 2002; Hastings *et al.*, 2005; Theoharides & Dukes, 2007; Lockwood *et al.*, 2013), but as for knotweeds, its effect is quite unknown.

5.4.2. Range, niche, and modelling knotweeds' dynamics

Our ability to fully understand and predict knotweed invasions is limited by the versatility of their dynamics at all scales. Furthermore, since knotweeds are extremely persistent and resilient, the best way to avoid their impacts is likely to prevent their arrival or to operate early detection and control (Child & Wade, 2000; Colleran & Goodall, 2014; Schifflerthner & Essl, 2016). Forecasting knotweeds' dynamics therefore appears to be a stake for both fundamental researches in biogeography and invasion ecology as well as for applied conservation and management. Hence the strong appeal observed in the last decades for the various methods of predictive modelling (Pyšek & Hulme, 2005; Meier *et al.*, 2014; Descombes *et al.*, 2016).

5.4.2.1. Models on knotweeds' dynamics

Over the years, 21 papers have proposed models to study various aspects of knotweeds in a wide range of scales and resolutions. Out of these, 5 presented models on the growth of clonal fragments (i.e. Suzuki, 1994a; Adachi *et al.*, 1996b; Smith *et al.*, 2007; Dauer & Jongejans, 2013; Lavallée *et al.*, Submitted) whose results have already been discussed (see section 5.3.1.2.). The remaining 16 models may be classified in two categories: Habitat Suitability Models (HSMs; $n = 13$), and *hybrid* models ($n = 3$).

What we refer to as HSMs regroup a set of species distribution modelling methods such as *climate envelope* models (e.g. Beerling *et al.*, 1995) or *environmental niche* models (e.g. Jovanović *et al.*, 2018), all based on a correlative approach (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Schurr *et al.*, 2012). These methods try to link the distribution of species to environmental predictors that are presumably constraining them. The philosophy behind HSMs is that, if measured at a sufficiently large spatial scale, the distribution of a species reflects its fundamental niche (Guisan & Thuiller, 2005; Soberón, 2007; Gallien *et al.*, 2010). If successful, HSMs can be used to predict the invasibility of uninvaded areas or study the response of species to global change scenarios, notably at large scale (Guisan & Thuiller, 2005; Gallien *et al.*, 2010). Substantially more sophisticated, hybrid models take advantage of

the accuracy potential at large spatial scales of HSMs while combining it to the ability of mechanistic models to implement dynamic situations and account for demographic processes (Gallien *et al.*, 2010; Meier *et al.*, 2014).

Regarding knotweeds, HSMs have been used at different scales⁴ and for various purposes. At the regional scale, for instance, they have showed that knotweeds are frequently associated with roads and rivers (Collingham *et al.*, 2000; Rouifed *et al.*, 2014), especially artificialized sections of rivers (Navratil *et al.*, 2018), but that their probability of presence is not affected by forests-induced shade (Duquette *et al.*, 2015; Descombes *et al.*, 2016). At larger spatial scales, HSMs have mainly used bioclimatic variables, sometimes with edaphic or *habitat* related predictors (e.g. Barney *et al.*, 2008; Chai *et al.*, 2016), usually to identify the climatic niche of knotweeds (e.g. Beerling *et al.*, 1995; Ainsworth *et al.*, 2002; Bouchier & Van Hezewijk, 2010), or to simulate their potential range dynamics under climate change (e.g. Beerling, 1993; Jovanović *et al.*, 2018). Most of these *continental* scale studies report that knotweeds have not yet reached their range limits and that increased mean temperatures will likely stretch their potential distribution even further (Beerling, 1993; Beerling *et al.*, 1995; Bouchier & Van Hezewijk, 2010; Jovanović *et al.*, 2018).

The three studies that used hybrid models on knotweeds all worked at the regional scale to predict the effect of various scenarios. Meier and colleagues (2014) tried to simulate the spread of *R. japonica* (along with *Impatiens glandulifera* and *Heracleum mantegazzianum*) over 15 years, “constrained by 361 control options differing in local intensity, area treated, treatment frequency, duration of treatments and spatial prioritization”. Among other things, they reported that for a similarly low pecuniary investment, early control is more effective than repeated control to contain invasions, and that large knotweed populations should be targeted in priority by eradication campaigns (Meier *et al.*, 2014). Carboni and others (2018) have used a hybrid model to assess the invasion risk of knotweeds and many other INPSs in a National Park of the French Alps under various scenarios of climate or socio-economical changes. They notably concluded that knotweeds occupancy in the National Park could more than double in the case of human-mediated propagule pressure increase, but that their invasion could be extremely limited if introductions were stopped (Carboni *et al.*, 2018). Finally, using a hybrid model (*sensu lato*) between a *dynamic vegetation model* and a *morphodynamic model*, van Oorshot *et al.* (2017) investigated the impact of *R. japonica* on riverbanks vegetation and hydrogeomorphology under two scenarios of propagule pressure but did not discussed the dynamics of the plant *per se*.

5.4.2.2. *Model calibration and predictive limitations*

The potential usefulness of predictive models is very high, yet it is also strongly constrained by several statistical, conceptual and practical limitations (Collingham *et al.*, 2000; Hulme, 2003; Guisan & Thuiller, 2005; Dormann, 2007; Gallien *et al.*, 2010). Models on knotweeds' dynamics are no exception. On the contrary, some of these limitations are particularly relevant for knotweed models and seriously affect the validity of their predictions.

⁴ The methods used to quantify the rate of spread of knotweeds or to predict their dynamics are similar for both what we called here the regional and the continental scales, it is therefore quite logical to discuss them together.

An obvious first problem arises from the quality of results and the trust we can have in them, and thus on models validation and the clarity of speech about it. Sometimes, the model is meant to be purely exploratory (e.g. van Oorschot *et al.*, 2017), and sometimes authors simply admitted failing to reach satisfactory results (e.g. Barney *et al.*, 2008; Pěkníková & Berchová-Bímová, 2016). A far more problematic situation emerges when no validation or accuracy assessment is reported at all (e.g. Beerling, 1993; Ainsworth *et al.*, 2002). Fortunately, in most studies, cross-validations are performed and validation metrics for the HSMs are provided, although often in Supplementary Materials and without explanations on the meaning of these metrics: e.g. True Skill Statistics (TSS), Area Under Curve (AUC), *k*-statistics. An additional problem stems from the inherent uncertainty of scenarios themselves (Dormann, 2007). One might regret that the way these predictions are reported often fails to reflect this intrinsic uncertainty.

At least three major problems linked to models' input data may lead to substantial inaccuracies:

- Firstly, taxonomic misidentifications may exist in the distribution data used in HSMs. The differentiation of knotweed species is famously difficult, notably between *R. japonica* and *R. x bohemica*, and many mistakes in distribution maps have already been observed (Zika & Jacobson, 2003; Bailey & Wisskirchen, 2006; Meerts & Tiébré, 2007; Tiébré *et al.*, 2007a; Sîrbu & Oprea, 2008; Pfeiffenschneider *et al.*, 2014). Recently, Vuković *et al.* (2019) reported that *R. x bohemica* had been overlooked in the Balkan Peninsula and that the HSM from Jovanović and colleagues (2018) should be corrected. Similarly, distribution maps of knotweeds made by Jalas and Suominen (1979) are older than the first identification of *R. x bohemica* made in 1983. Works based on these maps should then be revised as well (e.g. Beerling, 1993; Beerling *et al.*, 1995).
- Secondly, species distribution data are often prone to spatial autocorrelation which may become an issue for many statistical approaches (Guisan & Zimmermann, 2000; Dormann, 2007). If some authors explicitly acknowledge this risk and use specific methods to account for spatial dependencies in the data (e.g. Meier *et al.*, 2014), many others seem to ignore this issue.
- Thirdly, the type and resolution of input data is extremely important for the quality and meaning of predictions (Hulme, 2003; Austin, 2007). To ensure relevant correlations, the spatial resolution of environmental variables should be equivalent to or finer than the resolution of the distribution data (Collingham *et al.*, 2000). Otherwise, there will be no correspondence between occurrences and environmental drivers. For instance, if knotweeds are mapped at a resolution of 1 km, only drivers that vary at a coarser resolution (e.g. climate, geology, human population density) can be meaningful to determine their distributional patterns. In a way, the size of the sampling units determines the type of niche that is modelled (Austin, 2007). Unfortunately, many studies on knotweeds seem to disregard these considerations.

Now, whether for classic HSMs or the HSM-components of hybrid models, the most problematic part is related to the underlying assumptions of HSMs. Good validation metrics indicate that a model is able to reproduce with a good accuracy the distribution of the studied

species using the input variables, in the same range as the calibrating data and at the same resolution. However, it definitely does not mean that the model is able to actually identify the potential range of the species (Dormann, 2007; Gallien *et al.*, 2010; Schurr *et al.*, 2012). It would only be the case if the species distribution is at equilibrium with its environment (Hulme, 2003; Guisan & Thuiller, 2005; Dormann, 2007). Yet, non-equilibrium dynamics are frequent for INPSs (Gallien *et al.*, 2010; Václavík & Meentemeyer, 2012), and possibly for knotweeds in most regions of the world (see next section). It is not because knotweeds are regionally widespread that they are close to occupy all suitable habitats. If due to dispersal limitations, species are frequently absent from suitable habitats, then HSMs and hybrid models will invariably underestimate their potential distribution (Guisan & Thuiller, 2005; Schurr *et al.*, 2012).

For this reason, it is often advised to calibrate HSMs using data from the INPSs' native range (Guisan & Thuiller, 2005; Gallien *et al.*, 2010; Elith, 2017). However, in their native ranges, knotweeds endure important herbivory (Bailey, 2003; Maurel *et al.*, 2013), pathogen attacks (Beerling *et al.*, 1994; Kurose *et al.*, 2013), and must compete with 'giant herb' communities (Sukopp & Starfinger, 1995). Therefore, chances are that the distribution of knotweeds in their native ranges is far more strongly constrained by biotic interactions than in their introduced range (Hulme, 2003), and that their introduced realized niche can potentially be larger than their native one (cf. Soberón, 2007; Alexander & Edwards, 2010; Gallien *et al.*, 2010; Guisan *et al.*, 2014). Moreover, native distributions do not take into account the potential genetic adaptation of populations to new conditions in their introduced range and thus shifts of their fundamental niche (Dormann, 2007; Alexander & Edwards, 2010; Gallien *et al.*, 2010), while knotweeds may have experienced such adaptation (Bailey *et al.*, 2007; Krebs *et al.*, 2010). We could furthermore ask ourselves where is the *native* range of *R. x bohemica*? Consequently, both native and introduced range should likely be included in large scale HSMs (Gallien *et al.*, 2010), which has never been done in knotweeds' modelling studies (but see Beerling *et al.*, 1995).

The mechanistic component of hybrid models is precisely designed to address several of these limitations. Because mechanistic models can partly account for dispersal, demography and competition for resources, they are theoretically less likely to underestimate the potential range dynamics of INPSs (Gallien *et al.*, 2010). But this is only true if the underlying processes and their interactions with environmental conditions are correctly understood and integrated. We have seen that knotweed spread involves (potentially but not necessarily) three different propagule types that may have differing dispersal curves (Figure 5), and that may produce juveniles characterized by very different establishment probabilities (Figure 2). Appropriately approximate such a complex expansion process in a model would likely be extremely difficult, and has not been attempted in existing models. On the other hand, existing hybrid models on knotweeds have parametrize situations that seem rather curious. In their model, Meier *et al.* (2014) considered that eradication of established knotweed populations was achievable by mimicking various intensities of mechanical or chemical treatments. However, knotweed eradication is very rarely observed, even when extremely intensive control options are applied (Child & Wade, 2000; Kabat *et al.*, 2006; McHugh, 2006; Delbart *et al.*, 2012). Quite similarly, no evidences of source-sink dynamics and competitive exclusion of

established knotweeds have ever been published (as far as we know), contradicting the predictions of Carboni *et al.* (2018). This discrepancy between theoretical expectations and predictions may have several (non-exclusive) explanations linked to the intrinsic limitations of the various components of hybrid models (for a review, see Gallien *et al.*, 2010).

5.4.2.3. *Niche breadth and range dynamics of knotweeds*

Most HSMs on knotweeds have been calibrated using only a part of their introduced range. An implicit assumption behind this is that knotweeds had time, in this partial range, to disperse repeatedly to most suitable habitats and thus to be approximately at equilibrium with their environment. If not, then any prediction from a HSM would underestimate the species potential range (Guisan & Thuiller, 2005; Schurr *et al.*, 2012). Curiously, this *closeness to equilibrium* hypothesis is rarely challenged in the papers presenting HSMs (Araújo & Pearson, 2005). Therefore, one may ask: are knotweeds likely to be often at equilibrium with their environment in their introduced range (or part of it)? To answer this question, it is convenient to rely on the niche concept.

In demographic terms, a species niche represent those environments for which its population growth rate is positive (Pulliam, 2000; Schurr *et al.*, 2012), which means that the species can persist without immigration (birth > death). The distribution of a species (Figure 7) is at the intersection of (A) the geographic area where abiotic conditions enables the species to live indefinitely (i.e. the *fundamental niche*; Pulliam, 2000), (B) the geographic area where the species can coexist with or exclude competitors, and (M) the geographic area that has been or is accessible to the species (e.g. since its introduction). The portions of space where these three areas overlap (R) represent the *realized niche* (Soberón, 2007; Alexander & Edwards, 2010; Gallien *et al.*, 2010), that is where the species occurs and has a positive population growth rate. Now, the aim of HSMs is to estimate the *potential range* (*pr*) of the species ($pr = P + R$; with P the *potential realized niche*), by correlating a subset of the species distribution in R with environmental variables possibly representing the conditions A (abiotic drivers: e.g. climate, soil) and B (biotic drivers: e.g. vegetation types) of R. If the species is at equilibrium, then the sampled values of the environmental variables may be representative enough to get a good approximation of *pr* (Figure 7b). On the other hand, Figure 7c possibly better represents the introduced range of knotweeds and HSMs attempts for at least three reasons: (i) knotweeds experienced a shift in their *realized niche* (already suggested in the previous section); (ii) they suffer from strong dispersal limitations (see below); (iii) studies that only use part of knotweeds introduced range deprive their datasets from useful chunks of information on the abiotic and biotic dimensions of the niche (e.g. if you only use the Benelux distribution of knotweeds, you will not be able to predict the presence of knotweeds in mountains, or in the arctic, or in the Mediterranean region).

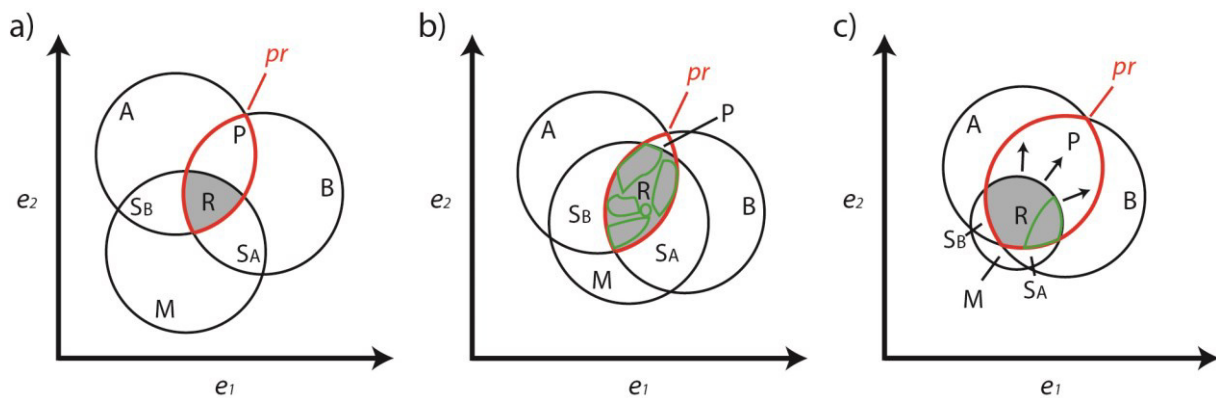


Figure 7. Heuristic representation of (a) the geographic range of a species in a simplified niche space (modified from Soberon, 2007 and Alexander & Edwards, 2010). A represents the geographic area of the abiotic niche (or fundamental niche). B represents the geographic area of the biotic niche. M represents the geographical extent that the species managed to reach through dispersal throughout its life history. Consequently, R represents the species realized niche, P the species *potential* realized niche, and *pr* its potential range. S_A represents areas where we can find *sink* populations due to unsuitable abiotic conditions. S_B represents areas where we can find *sink* populations due to unsuitable biotic conditions. In (b) is depicted the theoretical situation assumed by most HSMs on knotweeds (where green areas represent the sampled distributions used in the models), while (c) may actually be more close to the actual situation of knotweeds' invasion (arrows representing future range expansion delayed by current dispersal limitations).

Over the years, countless papers have reported the “habitat preferences” of knotweeds, although only few actually quantified such preferences. Mostly, they indicate that knotweeds are preferably found at low elevation in open, rich, humid, disturbed and/or polluted areas such as wastelands, industrial and residential areas or along roads, railways, wood margins and rivers (e.g. Beerling *et al.*, 1994; Palmer, 1994; Sukopp & Starfinger, 1995; Mandák *et al.*, 2004; Tiébré *et al.*, 2008; Chmura *et al.*, 2013; Liendo *et al.*, 2016). In contrast, there are comparatively very few records or observations of knotweeds in more natural, undisturbed and/or secluded habitats (e.g. open or closed-forests, grasslands, mountains) even if the trend may be increasing (e.g. Bailey & Wisskirchen, 2006; Tiébré *et al.*, 2008; Clements & DiTommaso, 2012; Roufied *et al.*, 2014; Dommaget *et al.*, 2016; Wilson *et al.*, 2017; Martin *et al.*, 2019). This overwhelming imbalance has obviously led some people to consider that the presence of knotweeds is restricted to the former type of habitat and, by extension, that their distributions are at equilibrium and have qualitatively almost reached their niche limits (as in Figure 7b). A corollary is that knotweeds in the latter type of habitats do not exist or represent sink populations (i.e. belong to areas S_A and S_B in Figure 7).

However, it is likely that in most regions of their introduced range, knotweeds are still expanding, notably in less anthropized habitats, but perhaps in a slower and less obvious fashion (secondary invasions; cf. Dietz & Edwards, 2006). Residence time, dispersal constraints and thus differences in propagule pressure between habitat types would therefore explain the misleading appearance of absence in certain favourable areas. Propagules have indeed far more chances to be introduced and carried around in, for instance, a low elevation floodplain or urban area than in a forest or at high elevation. But it does not mean that knotweeds could not thrive in such places. Strong shade (and thus competition for light) prevents knotweed seedlings establishment (see section 5.2.3.), but it does not impede

juveniles born from fragments to establish, grow, bloom and potentially provide new vegetative fragments (Descombes *et al.*, 2016; Dommanget *et al.*, 2019; Martin *et al.*, 2019; Martin *et al.*, in prep.). From this point of view, knotweeds living in forests may be viewed as being in their niche (cf. Pulliam, 2000). Other aspects of competition and interactions between them may exclude knotweeds, but probably not light availability alone as considered in several modelling studies (e.g. Carboni *et al.*, 2018; Navratil *et al.*, 2018). Likewise, and similarly to other INPSs (Pauchard *et al.*, 2009; Alexander *et al.*, 2011), recently reviewed evidences suggest that knotweeds could thrive in mountains (up to a certain limit, of course) provided that propagules are dispersed there (Martin *et al.*, 2019). In other words, the rarity of knotweeds in mountain regions is more likely explained by a lack of dispersal opportunities due to a short residence time rather than by physiological limitations. Therefore, knotweeds' potential realized niche and potential range may have been, here again, underestimated.

5.5. THE CONTINENTAL SCALE

Due to the already great length of this review, we decided not to address the invasion dynamics of knotweeds at the continental/global scale. Still, we believe that various aspects of these very large-scale dynamics and patterns are worth discussing, such as: the link between introduction history across continents and large-scale patterns of distribution; continental patterns of taxa and ploidy levels' distributions and the identification of *evolutionary hotspot* regions; and the effect of climate change on the potential distribution of knotweeds.

5.6. DISCUSSION

We have seen throughout this review that the invasion dynamics of knotweeds occur in a nested hierarchy of spatiotemporal scales. The *infilling* of each of these scales is carried out by different processes: i.e. establishment at the *micro-local* scale, clonal expansion and short-distance dispersal at the *local* scale, and long-distance dispersal at the *regional* scale. In this hierarchy of simultaneous dynamics, levels are not independent (cf. Pyšek & Hulme, 2005; Theoharides & Dukes, 2007). It means that the spatiotemporal patterns of a given level are in fact the sum of all the patterns occurring on lower levels but can also be influenced by higher level processes; e.g. when the establishment of a juvenile is facilitated by the growth of an older clonal fragment (through niche construction) or suppressed by it (due to intraspecific competition), or when the infilling of a site is enhanced by the introduction of new propagules coming from distant populations.

All these processes can be characterized by *rates* (e.g. rate of success, rate of expansion), and estimating these rates and their fluctuations is, in a way, the key to predict the outcome of knotweeds invasions across scales. Yet, these process rates are controlled by different drivers:

- Establishment success depends on both abiotic (adequate climate and soil humidity) and biotic conditions (mostly competition for light), but the influence of these drivers

probably strongly varies with the type and size/weight of the propagules that gave birth to establishing juveniles.

- Rate of clonal (lateral) expansion appears to be dependent on the age of individuals, but is also influenced by environmental conditions (e.g. light availability, obstacles).
- And frequencies of short and long distance dispersal mostly depend on propagule pressure and dispersal opportunities.

Two important conclusions can be drawn from these observations. Firstly, the clonal nature of knotweeds is central in their invasion dynamics (i.e. to enhance establishment success; to occupy and dominate communities; to persist in the wait of opportunities; to multiply the possibilities of dispersal and affect the distance of transport), and should not be overlooked. Secondly, the role of disturbances such as floods, vegetation management operations or construction works is paramount in the variability of all these processes (by providing establishment opportunities; by influencing clonal growth; and especially by being the main type of dispersal opportunities), possibly exceeding by far the role of most other drivers. However, it does not mean that knotweeds are completely idle without disturbances.

We acknowledge that the definitions and limits of the various scales and processes addressed in this paper may be debatable and perfectible. Most choices have been made for writing convenience and because a conceptual framework that explicitly integrates the movements of INPSs across hierarchical spatiotemporal scales while accounting for the specificities of clonal plants (e.g. multiplicity of propagule types and strength, ability to expand laterally or even move, ability to select habitats, absence of compulsory sexual reproduction, extreme persistence) is still lacking. An additional complication is the fuzziness and lack of clear definition behind various terms and concepts (e.g. dispersal, establishment, dynamic, scale) as already emphasized by others (Camus & Lima, 2002; With, 2002; Gurevitch *et al.*, 2016). More efforts are probably required to address this conceptual challenge, but interesting avenues may perhaps be found in works related to the *hierarchy theory* (cf. Allen & Starr, 1982; O'Neill *et al.*, 1986).

5.6.1. General insights and scale-dependent research perspectives

We hope that the critical and up-to-date synthesis presented here will be useful to improve our ability to predict the dynamics of these plants across scales and design better management strategies. However, to reach these goals, several knowledge gaps should certainly be addressed, and some key aspects of the spatiotemporal dynamics of knotweeds should be re-emphasized.

The potential of regional or continental models is huge, whether to predict, understand, or to prioritize management operations. However, modelling techniques involve various pitfalls. One of the main interests of this review is perhaps that it highlighted some of them as relevant for knotweeds, enabling improvements in the conception of models (cf. Gallien *et al.*, 2010). For instance, considerations about regional patterns (of taxa distribution, ploidy levels etc.), temporal biases and absence of equilibrium could now be accounted for by correlative models. Similarly, mechanistic models could certainly benefit from the data presented here or

more simply from the insights gained on key spatiotemporal processes discussed throughout this paper. However, it appears that there is a need to better assess the potential niche of knotweeds and their range limits. To date, if we exclude HSM studies, only one study explicitly addressed this question (Seipel *et al.*, 2016). Although their results on knotweeds might be subject to caution (see Martin *et al.*, 2019), Seipel and colleagues elegantly tried to quantify the population turnover rates of INPSs along an elevational gradient to find the threshold beyond which, death exceeds birth. Such idea could be repeated or extended to other environmental gradients. Yet, the clonality of knotweeds should not be ignored and measures of the niche should account for vegetative multiplication (and persistence of ramets through time) and not only for sexual reproduction (Harper & White, 1974; de Witte & Stöcklin, 2010). It would also be interesting to test the viability of the clonal propagules produced in *less favourable* habitats (e.g. in forests). Additionally, the potential of knotweeds for genetic adaptation as well as for epigenetic variations should certainly be the focus of more research efforts as it may enhance the fitness of these plants (Richards *et al.*, 2012; Parepa *et al.*, 2014; Douhovnikoff & Dodd, 2015; Gillies *et al.*, 2016) and thus, their niche widening.

Many grey areas have punctuated the scale-continuum we reviewed in this paper, highlighting several research perspectives:

- At the *micro-local* scale, the most pressing question is probably to define the actual shape of the curves depicting the probability of survival as a function of environmental harshness for the juveniles born from rhizome and stem fragments, and how this relationship varies with the size/weight of fragments (cf. Figure 2) and between genotypes. It would also be interesting to learn more about the dormancy abilities of the various types of propagule.
- At the *local* scale, it clearly appears that the modalities of the clonal growth of knotweeds need further study, especially in the long term. Are knotweeds truly able to choose their habitat? How fast is the lateral spread of knotweeds? Is it monotonous? How is it influenced by environmental conditions and heterogeneity? Are knotweeds *mobile*? Are they able to operate division of labour? What is the maximal distance of clonal integration between ramets? What is the longevity of rhizome connexions? Does mowing truly favour the lateral expansion of clonal fragments? When are buds sinks and thus, when are pesticides able to kill them (Bashtanova *et al.*, 2009)? The number and variety of these questions illustrate the important gaps currently existing in our understanding of knotweeds clonal dynamics. Filling these gaps could help predicting the evolution of invaded sites and design better management strategies: e.g. by containing or orientating the growth of clonal fragments.
- At the *regional* scale, substantial efforts should be made to acquire data on the distribution of knotweeds and its changes through time. Remote sensing could be a very useful approach to provide cost-efficient very high resolution data on knotweeds at large spatial scale, provided that recent results can be satisfactorily up-scaled (Müllerová *et al.*, 2017; Martin *et al.*, 2018). Both early detection and spatiotemporal monitoring could benefit from these techniques. However, an important drawback is the impossibility to differentiate the various knotweed taxa, and the difficulty to detect knotweeds growing under the canopy of trees (but see Müllerová *et al.*, 2017).

Whatever their origin, more data on the spatial and temporal dynamics of knotweeds are essential to gain more profound insights into the long-distance dispersal of knotweeds, or to validate mechanistic (or hybrid) models and therefore improve our ability to predict their regional expansion.

Overall, we do not know much about the effect of environmental heterogeneity on the dynamics of knotweeds or about the possible effects of climate change, whatever the scale. Addressing these points would certainly not be useless.

Besides, because of insufficient data, the present synthesis has globally ignored the dynamics of the much less widespread *Fallopia x conollyana* J.P. Bailey (hybrid progeny of *R. japonica* and *F. baldschuanica*; Bailey, 2001). Still, we advise watchfulness regarding this taxon as its number of records is slowly increasing in Europe (e.g. Bailey & Spencer, 2003; Holm *et al.*, 2017; Hoste *et al.*, 2017).

5.6.2. Lessons for management

Despite the persistence of many unknowns, we believe that the portrait we drew of the invasion dynamics of knotweeds can be quite useful to reaffirm management preconisation or to express new ones.

Considering that even regenerating ramets can endure several events of destruction of their aboveground organs (Martin *et al.*, in prep.), early control operations should therefore favour hand-pulling rather than cutting/mowing (Colleran & Goodall, 2014; Barthod & Boyer, 2019).

For established populations, repeated careful and timely actions can be applied in areas where knotweeds cause troubles, notably just before flowering to prevent risks of seed production (Bram & McNair, 2004). Cutting/mowing operations should then be applied on the entirety of stands to ensure better effects (Martin *et al.*, in prep.). For undisturbed and thus un-dynamic stands, management is not necessarily advised unless one wants to avoid these stands to act as future dispersal foci. In any case, mowing/cutting residues should be disposed appropriately to avoid further spread (cf. Crowhurst, 2006; Barthod & Boyer, 2017). Locally, management by restoration of competitive native species can be a very interesting solution, sometimes in association with cutting in the first years to ensure restoration success (Dommanget *et al.*, 2015; Dommanget *et al.*, 2019). This solution could be particularly useful in riparian corridors as it would offer the twofold advantage of limiting the vigour and clonal spread of knotweeds, and strengthen riverbanks against erosion and thus decrease the number of dispersed propagules during floods.

At the regional scale, HSMs could be used to help prioritize early detection efforts, while keeping in mind their limitations (Theoharides & Dukes, 2007). For this reason, we would like to re-emphasize that the slowness of knotweeds' *secondary* expansion dynamics should not be mistaken for weakness or ill-adaptation when it is certainly only a matter of dispersal opportunities. One more time, it should be stressed that the temporality of dynamics of a potentially immortal organism has many chances to be unfit for the judgement of humans. We could say that knotweeds are very patient. When they manage to establish, they become

almost impossible to remove (Child & Wade, 2000; Kabat *et al.*, 2006; Delbart *et al.*, 2012). Underestimating knotweeds, whether in modelling studies or in any other forms of scientific communication, may thus have important consequences in terms of conservation and management. Even small and subordinated (not dominant) stands of knotweed represent considerable propagule banks and potential dispersal foci. Consequently, even isolated and un-dynamic populations should be dealt with care because timely disturbances may suddenly expand them and/or grant them dominance. As such, we could perhaps consider that knotweeds hold an *impact debt* at the regional scale. Consequently, prevention in order to avoid the colonisation of still preserved regions (e.g. mountains, rural or isolated areas, islands), habitats or ecosystems should be a top priority.

Overall, the multiscale hierarchical nature of knotweeds dynamics should not be ignored by managers and decision makers as it is of prime importance for a successful management at any scale. For instance, trying to eradicate knotweeds in a site is useless if the site is frequently repopulated from outside. This is why river management should start upstream to go downstream (Dawson & Holland, 1999; Schifflerthner & Essl, 2016), and the preservation of mountains (but it is likely relevant for any uninvaded area) should incorporate lower adjacent regions (McDougall *et al.*, 2010). For this purpose, coordination among stakeholders is essential (Kabat *et al.*, 2006; Braun *et al.*, 2016), and so is public awareness. Efforts to limit disturbances, especially anthropogenic ones, should also be undertaken (Theoharides & Dukes, 2007). As knotweeds expand very little without disturbances, it means that controlling disturbance regime may possibly lead to the quarantining of knotweeds populations or metapopulations.

Finally, in regions or countries that are not yet strongly invaded (e.g. Chile, South Africa, Alaska, central US regions, possibly also Australia and New Zealand) the eradication of knotweeds is still certainly feasible. And since re-introductions are probably far less likely than before, it could be an opportunity to cross for good the names of knotweeds from regional INPS lists.

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– ABSTRACT –

Although less mediatized than deforestation or climate change, biological invasions remain problematic for the conservation of many ecosystems and the maintenance of various socio-economical activities.

Understanding the way invasive non-native species spread in their introduced range is enabling a better apprehension of their impacts, the possibility to predict their expansion, and the development of better management strategies. A problem is that a species invasion dynamics are actually composed of a hierarchy of processes occurring simultaneously at various spatiotemporal scales and which are controlled by drivers that are time- or context-dependent. To gain more profound insights into these dynamics, one has to study the patterns they create and their underlying processes at all relevant scales.

Occurring on the five continents and highly invasive on at least two of them, Asian knotweeds (*Reynoutria spp.*) are acknowledged as being among the most invasive species in the world. Gifted with a large environmental tolerance and high abilities for vegetative multiplication, these giant herbaceous plants can quickly form large clonal monocultures that exclude the other plant species, modify biogeochemical cycles, and affect various anthropic activities. Target of management campaigns for decades, knotweeds display an insolent resilience to the great despair of many stakeholders. Despite having been extensively studied, many aspects of their dynamics are still elusive. Consequently, in this thesis, we have tried to *highlight what the drivers of the spatiotemporal dynamics of knotweeds across scales are, and how their management could benefit from a better understanding of these dynamics?*

To answer these questions, we first focused our attention on the clonal dynamics of knotweeds and on their variations when they experience differing conditions in terms of light availability and disturbance (repeated mowing). We have shown that although shade or mowing affects the vigour and the development of clones, it does not prevent their establishment or their growth. In fact, knotweeds seem able to adopt different growth strategies to cope with environmental heterogeneity, suggesting some management avenues. In a second study, we tried to identify the drivers that controlled the expansion of knotweed stands along an elevational gradient. If we showed that the lateral expansion of stands is mostly constrained by their size (and thus, possibly their age) and the vicinity of roads and rivers, we also brought evidences that knotweeds could have the potential to invade mountain regions. Then, to help for the acquisition of large-scale datasets on knotweeds' distribution, we developed a procedure to accurately detect and map knotweeds using satellite or drone imagery. Our results were quite encouraging and could be useful to both the basic research

and to the detection of newly invaded areas, enabling earlier control operations and more efficient management.

Finally, we tried to draw a full picture of the current knowledge on the invasion dynamics of knotweeds by reviewing the literature on the movement of these plants across spatial and temporal scales, to discuss and expand the reach of the insights gained in the various chapters of this thesis.

– RESUME –

Bien moins médiatisées que la déforestation ou le changement climatique, les invasions biologiques n'en demeurent pas moins problématiques pour la conservation de nombreux écosystèmes ou le bon déroulement de nombreuses activités socio-économiques.

Comprendre la façon dont les espèces exotiques envahissantes s'étendent dans les différents milieux qu'elles colonisent c'est permettre à la fois de mieux appréhender leurs impacts, de pouvoir prédire leur expansion, et de trouver les endroits stratégiques où agir pour contrer ou atténuer les effets indésirables de ces espèces. Le problème est que les dynamiques d'invasions d'une espèce regroupent en fait une hiérarchie de processus se produisant simultanément à différentes échelles spatiotemporelles et qui sont contrôlés par des facteurs qui changent en fonction du temps et du contexte d'invasion. Pour acquérir une compréhension profonde de ces dynamiques, il faut donc étudier leurs manifestations et leurs causes aux diverses échelles spatiales et temporelles auxquelles elles se produisent.

Présentes sur les cinq continents et très envahissante sur au moins deux, les renouées asiatiques (*Reynoutria spp.*) sont reconnues comme faisant partie des espèces les plus invasives de la planète. Dotées d'une grande tolérance environnementale et d'importantes capacités de multiplication végétatives, ces plantes herbacées géantes peuvent former rapidement de grandes monocultures clonales qui excluent les autres espèces végétales, modifient les cycles biogéochimiques des zones envahies et perturbent diverses activités anthropiques. Cibles de campagnes de gestion depuis des décennies, elles affichent cependant une résilience insolente qui désespère de nombreux gestionnaires. Bien que très étudiées, de nombreux détails concernant leurs dynamiques nous échappent toujours. Dans ce travail de thèse, nous avons donc cherché à *identifier quels sont les facteurs qui contrôlent les dynamiques spatiotemporelles des renouées à différentes échelles, et comment une meilleure compréhension de ces dynamiques clés pourrait profiter à leur gestion ?*

Pour ce faire, nous nous sommes donc d'abord intéressés à leur dynamiques clonales et à leurs variations en fonction de différentes conditions de stress (ombrage) ou de perturbation (fauchage répétée). Nous avons montré que si les renouées sont bien affectées par des conditions stressantes ou perturbées, cela ne les empêche ni de s'établir, ni de croître. En fait, les renouées semblent pouvoir adopter différentes stratégies de croissance pour pallier ces contraintes, soulevant différentes questions liées à la gestion. Dans une deuxième étude, nous avons cherché quels étaient les variables qui expliquaient l'expansion des taches de renouées le long d'un gradient altitudinal. Si nous avons montré que les dynamiques d'expansion des taches étaient principalement contrôlées par leur taille (et donc potentiellement leur âge) ainsi que par la proximité de routes et de rivières, nous avons également apporté des indices

qui suggèrent que les renouées pourraient être potentiellement capables d'envahir les montagnes. Ensuite, pour tenter d'aider à résoudre le problème de l'acquisition des données de distribution des renouées à large échelle, nous avons développé une méthode pour détecter et cartographier les populations de renouées à partir d'images satellites et issues de drones. Notre méthode a montré des résultats encourageants et celle-ci pourrait être utile à l'étude des invasions ainsi qu'à la détection des nouveaux foyers d'invasion pour une gestion plus précoce et efficace des renouées.

Enfin, nous avons tenté de dresser un portrait global de la compréhension actuelle des dynamiques d'invasion des renouées en réalisant, en guise de discussion, une grande revue de littérature sur les mouvements de ces plantes à travers les échelles spatiales et temporelles et en y intégrant les apports des autres travaux de cette thèse.