A Comparative Literature Review of the Ecological and Socioeconomic Factors Influencing the Establishment and Invasion of *Rhododendron ponticum* in Ireland and *Hydrocotyle ranunculoides* in the Netherlands

Bachelor's Thesis Earth and Environment
University College Utrecht
Áine Coakley (#6496725)

Supervisor:
Dr. Kees Klein Goldewijk

Date:
09/08/2025

Word count:
7590

Universiteit Utrecht

Summary

Biological invasions represent a growing threat to global biodiversity, ecosystem functioning, and socio-economic stability. Despite extensive research on invasive species, comparative studies that analyse how ecological and socio-economic factors interact across contexts remain scarce. This thesis investigates how combinations of biological traits, habitat characteristics, and human-mediated introduction pathways influence the establishment and spread of invasive plant species. Using the Macroecological Framework for Invasive Aliens (MAFIA) established by Pyšek et al. (2020), I conduct a comparative literature review of two invasive plant species: *Rhododendron ponticum* in Ireland and *Hydrocotyle ranunculoides* in the Netherlands.

The central research question behind this analysis is: How can insights from historical plant invasions in Europe inform more accurate prediction and management of future invasions? To answer this, I examine the role of species traits, local environmental conditions, propagule pressure, residence time, and socio-economic drivers in shaping invasion outcomes.

The analysis demonstrates that while both species share biological and ecological characteristics typically associated with invasion success, such as rapid growth, high reproductive capacity, and tolerance of disturbance, context determines the magnitude and nature of their impacts. *Rhododendron ponticum* thrives in Ireland's acidic woodlands and established itself through centuries of intentional planting and weak early regulation (Dehnen-Schmutz et al., 2006). Its spread has resulted in significant biodiversity loss and long-term management costs, exceeding €1.5 million annually in Ireland alone (Dehnen-Schmutz et al., 2003). *Hydrocotyle ranunculoides* colonised Dutch waterways via the ornamental plant trade and has become a major economic burden due to its interference with water infrastructure and increased flood risk

(Baas & Duistermaat, 1998). Dutch control costs are projected to surpass €10 million by 2035 if spread continues unchecked (Diagne et al., 2020).

These findings demonstrate that invasion success cannot be reliably predicted through species traits alone. Effective management must incorporate context-dependent factors such as habitat vulnerability, socio-economic behaviours, and policy enforcement. Historical invasion data, when analysed through structured frameworks like MAFIA, can significantly improve future invasion risk assessments. The thesis concludes that effective prevention and management of invasive species require early detection systems, regulation of introduction pathways, ecological restoration of vulnerable habitats, and strengthened cross-border collaborations across Europe.

Introduction

The steep rise in global trade, travel, and human-mediated landscape alteration in recent decades has led to a corresponding increase in the introduction of non-native species into new environments (Seebens et al., 2020). While many of these introductions remain ecologically benign, with little effect on the health of their new ecosystems, some species establish self-sustaining populations and spread aggressively, often at the expense of native biodiversity. These are classified as *invasive species*. Invasive species can disrupt native ecosystems, alter species composition, and reduce ecosystem services (Kumschick et al, 2015). Consequently, they are now recognised as one of the leading drivers of global biodiversity loss (Blackburn et al., 2019; Bellard et al., 2016). In addition to ecological damage, invasive species can present significant economic burdens and pose risks to human health, particularly when costly eradication or management efforts are required (Cuthbert et al., 2022; Ogden et al., 2019).

In this review, I will compare and contrast the factors that influence the establishment of two invasive plant species in Ireland and the Netherlands. *Rhododendron ponticum* is one of the costliest and most damaging invasive species in Irish and British ecosystems, while in the Netherlands it has yet to cause significant problems, though its invasive potential has been recognised (Casati et al., 2023). In the Dutch waterways, *Hydrocotyle ranunculoides* has established itself as one of the most problematic invasive species, while it remains unestablished in Irish ecosystems, though similarly has been recognised as a potential threat (Millane et al., 2014; Djeddour et al., 2017). By comparing these two cases, this review aims to identify the factors that contribute to the successful establishment and spread of invasive species and evaluate how these factors vary between contexts. Such an analysis may inform better prevention and management strategies for future invasions across Europe.

Research gap and research question

The central research question of this review is as follows: "How can insights from the historical invasions of *Rhododendron ponticum* in Ireland and *Hydrocotyle ranunculoides* in the Netherlands inform predictive models of future plant invasions?" While risk evaluations of invasive species are common, they often lack a unified analytical approach and may overlook the interplay of context-dependent factors (Wilson et al., 2020; Catford et al., 2022). This review applies the MAFIA (Macroecological Framework for Invasive Aliens) developed by Pyšek et al. (2020) to conduct a comparative case study of *R. ponticum* and *H. ranunculoides*, aiming to demonstrate how a standardized framework can improve predictive capacity in invasion biology.

The importance of invasive species

The frequency and severity of biological invasions are increasing globally as human activity leads to a steadily more interconnected world (Li & Yu, 2023). New established alien species are being recorded worldwide at an unprecedented rate of 200 per year (Li & Yu, 2023). Furthermore, the total number of established alien species worldwide is projected to increase by 36% from 2005 through to 2050 (Seebens et al., 2020).

Damages incurred by biological invasions are also increasing with this rise (Cuthbert et al., 2022,). In terms of human health, invasive plant species such as Giant Hogweed (*Heracleum mantegazzianum*) carry risks of injury due to phytophotodermatitis (Baker et al., 2017). Invasive animal species, such as the Asian tiger mosquito (*Aedes albopictus*), present significant risks as vectors for illnesses such as dengue, LaCrosse and West Nile virus (Benedict et al., 2007). Economically, studies demonstrate that since 1960, management costs for biological invasions totalled at least $95.3 billion US dollars, while damage costs totalled at least $1130.6 billion US dollars (Cuthbert et al., 2022). Cuthbert et al. (2022) also found that these costs are increasing rapidly over time.

Biological invasions evidently can have significant ecological and economical effects that necessitate the understanding of the processes that facilitated them, as well as the underlying biological or evolutionary characteristics of the species that may have contributed to their success. This understanding is crucial in order to better predict and prevent new invasions, as well as allowing for improved management and control of current invasions.

Literature Review

Invasive Process

In order for a species to establish itself in a region and become invasive, it must survive various transitions (Gioria et al., 2023; Blackburn et al., 2011; Briski et al., 2018). It must initially enter via a pathway, i.e. be inadvertently transported via some human-mediated means from its region of origin to a new region (Blackburn et al., 2011). Having been introduced, it may then, through naturalisation, become *casual* to a region, which is the term given to species that are unable to maintain self-sustaining populations but are occasionally found beyond cultivation (Keller et al., 2011; Richardson et al., 2000). A species is established if it then propagates itself without human intervention (Keller et al., 2011). Blackburn et al (2011) proposed a unified framework that identifies the four key stages of invasion as: 1) transport, 2) introduction, 3) establishment and 4) spread. The term "invasive" is itself contested, with some arguing for a definition strictly based on ecological and biogeographic criteria, while others argue that only alien species with negative impacts should be described as invasive (Richardson et al., 2011; Richardson et al., 2000). In this review, a species is described as invasive if its spread and establishment cause measurable negative impacts, to the environment, economy or human health (Keller et al., 2011).

Driving factors for invasions

Competing theories further debate the contribution of different factors to the invasive potential of a non-native species. Charles Elton, often described as the founder of invasion biology, proposed the biotic resistance hypothesis, which holds that regions with high biodiversity and relatively low levels of disturbance, in particular caused by humans, will be more resistant to establishment by non-native species (Elton, 1958). While intuitively logical, studies have demonstrated that the reality is far more complex (Alpert et al., 2000; Blackburn et al., 2011; Briski et al., 2018; Catford et al., 2022, Hayes et al., 2008). Negative associations have been found between native and invasive species diversity at small scales, however positive associations can be found at larger scales (Ackerman et al., 2017). Contention in the field of invasion biology is also present in the applicability of some of the primary hypotheses that have been proposed to explain and predict biological invasions (Jeschke et al., 2012: Catford et al., 2009). Biotic resistance is one of these, with other hypotheses including the island susceptibility hypothesis, invasional meltdown hypothesis, novel weapons hypothesis, enemy release hypothesis, and the tens rule (Jeschke et al., 2012). One study that evaluated these hypotheses suggests that empirical support for some of them is doubtful and has declined over time, indicating the need for more rigorous research and consideration of broader biogeographical and socioeconomic contexts and their interactions with non-native species traits in the assessment and management of potentially invasive species (Jeschke et al., 2012).

Invasive Potential

Different factors that contribute to a species' invasive potential. Broadly, three primary categories of factors can be found in the literature. These include biological/genetic characteristics of the non-native species, location characteristics of the invaded area, and factors related to the introduction events of the species (Pyšek et al., 2020).

Biological factors

Several studies have investigated the importance of biological traits in relation to a species' invasive potential (Gioria et al., 2023; Hayes et al., 2008). The role of such traits has been shown to be highly context dependent, however (Kikvidze et al., 2011; Catford et al., 2022). Context dependence is a contested term in invasion biology that is widely invoked to explain differing results due to the conditions under which an effect is observed (Catford et al., 2022). Often, biological traits have been mistakenly identified as having contributed to invasion success (Pyšek et al., 2020). Traits that have been shown to play a role include seed bank persistence, fecundity, germination characteristics, karyological characteristics, high maximum relative growth rate and high resource allocation to shoots and leaves (Pyšek et al., 2009; Keller et al., 2011; Gioria et al., 2023).

Location factors

The effect of location characteristics on the invasive potential of a non-native species are also significant (Pyšek et al., 2009). The concept of 'invasibility' was described by Lonsdale (1999), as a 'regions vulnerability to invasion'. Factors that characterise an invasible habitat include its structure (i.e environmental conditions and native biota), the resource availability (i.e nutrient or water supplies present), and the level of disturbance of the habitat (Alpert et al., 2000). Further, the size of a species' native range has also been demonstrated to be significantly positively correlated to its invasive success (Pyšek et al., 2009; Hui et al., 2011).

Introduction and event related factors

Some of the clearest predictors of invasion success, however, are factors related to introduction events (Keller et al., 2011; Hayes & Barry, 2008). These include propagule pressure, colonisation pressure, residence time, and other socioeconomic factors that mediate pathways of introduction. The most significant of these are propagule pressure and residence time (Cassey et al., 2018, Keller et al., 2011; Hayes & Barry, 2008). Propagule pressure refers to the number of introduced individuals of a species to a non-native habitat, while residence time refers to the length of time for which a species has been present in a non-native habitat. High propagule pressure is associated with an increased ability of a species to overcome Allee effects and genetic bottlenecks that cause stochastic extinctions due to small population size (Pyšek et al., 2009, Gioria et al., 2023).

Another factor that particularly influences the likelihood of a non-native plant species establishing itself in a region is the introduction pathway that it travels to arrive. Introductions that occur through human socioeconomic activities, such as gardening, agriculture, forestry, trade and travel have been categorised into these pathways by various researchers (Hulme et al., 2008). They influence the assembly of non-native floras, the invaded niche, and ultimately the invasion success of non-native plants (Riera et al., 2024).

With so many variables, it is crucial to attempt to study invasive species in a contextually sensitive manner (Kikvidze et al., 2011). The development and use of invasion frameworks in this endeavour take as many contributing factors as possible into account in order to explain and predict invasive potential and invasive success (Pyšek et al., 2020; Blackburn et al., 2011).

Analytical Invasion Frameworks

Invasion science is as yet a relatively young discipline, which is evidenced in the recent development of many different frameworks whose general applicability have yet to be widely tested (Wilson et al., 2020). In order to choose an appropriate framework with which to evaluate *R. ponticum* and *H. ranunculoides,* different approaches to the study of invasions were compared.

The 'Tens Rule', as described by Williamson and Fitter (1993) holds that 1 in 10 of imported species appears in the wild, 1 in 10 of those introduced species becomes established, and that 1 in 10 of those established becomes a pest. This is a limited framework for describing invasions in the sense that it doesn't consider the mechanisms behind transitions, and is not spatially or contextually sensitive.

Various trait-based frameworks have also been utilised. The attempts of these frameworks to predict invader impacts on native species is based on the idea that alignment between the traits of native and invading species is central to understanding native species responses to invaders (Litt & Pearson, 2022; Ricciardi et al., 2013; Sih et al., 2010, 2011). They cannot, however, explain why non-invasive species share similar traits with invasive ones, and they often ignore contextual or human-mediated factors.

Blackburn et al. (2011) proposed a staged model for invasions that describes four stages (transport, introduction, establishment and spread) and assigns barriers to each stage. This framework is extremely useful for identifying barriers and transitions, but lacks a macro-level pattern analysis.

Pathway-focused frameworks, such as that proposed by Hulme et al. (2008), track pathways of introduction for different invasive species. This approach aims to prevent invasions at their source. While useful for policy and biosecurity, they don't explain why introduced species succeed.

MAFIA

In this review, I apply the Macroecological Framework for Invasive Aliens (MAFIA) developed by Pyšek et al. (2020) to compare the invasion dynamics of *R. ponticum* and *H. ranunculoide*s. The MAFIA framework emphasizes context dependence—that is, how the interaction of species traits, environmental characteristics, and introduction history influences invasion outcomes. Context dependence is a frequently invoked but inconsistently defined concept in invasion biology, often used to explain contradictory empirical findings (Catford et al., 2022). Pyšek et al.'s framework addresses this by analyzing large-scale invasion patterns using a standardised macroecological lens.

The framework considers the following elements within the three overarching categories of location factors, introduction/event factors and biological-ecological factors:

1. Donor species pool
2. Socioeconomic factors, propagule pressure, and colonization pressure
3. Residence time and spread potential
4. Biological traits of alien species
5. Characteristics of invaded habitats

By examining these interacting factors, MAFIA enables a more nuanced comparison of invasion processes across different species and regions.

Ireland: Invasion of Rhododendron ponticum

Fig 1. Rhododendron covering an area in the Knockmealdown mountains

(Irish Examiner, 2020)

Introduction and Spread

Rhododendron ponticum is one of the most expensive alien plant conservation problems to date in Ireland and Great Britain (Dehnen-Schmutz & Williamson, 2006). As the invasions in each country occurred simultaneously and began while Ireland was considered part of the United Kingdom, data pertaining to Great Britain shall also be included in this review. It was most likely introduced in Britain via the ornamental plant trade in 1763 from Spain (Dehnen-Schmutz & Williamson, 2006). The first description of its presence in Ireland dates to a plant in Dublin that was described as being “60 years planted” in 1834, while Hall and Hall describe large plants present in Derrycunihy Wood, Killarney in 1843 (Dehnen-Schmutz & Williamson., 2006).

Ecological and Economic Impact

The first descriptions of the ecological impact of *R. ponticum* in Ireland dates to 1911, where a group named the "international phytogeographical excursion" acknowledged its luxuriance in the Killarney Oakwoods as well as its non-native status, but gave no description of its impact on local biodiversity (Dehnen-Schmutz & Williamson, 2006). Since then, studies have demonstrated that bird populations are smaller in mature oak forests dominated by *R. ponticum* (Jones, 1972). Further, there are very few insect species associated with the plant, and its dense understory allows only about 2% of light through, which outshades native plant species (Malo et al., 2012; Casati et al., 2022).

The first documented control work of *R. ponticum* was undertaken by the Forestry Commission in the 1930's, and in 1981 work camps for volunteers were set up in Killarney National Park dedicated to the eradication of *R. ponticum*, which have continued annually since (Dehnen-Schmutz & Williamson., 2006).

The Netherlands: Invasion of *Hydrocotyle ranunculoides*

Fig 2. Hydrocotyle ranunculoides photographed by Johan van Valkenburg (NVWA 2024)

Hydrocotyle ranunculoides L.f., commonly known as floating pennywort in English or grote waternavel in Dutch, is a stoloniferous, perennial aquatic plant native to North America, ranging from Pennsylvania to Florida and as far west as Washington (EFSA, 2007; Djeddour, 2017). Once valued in aquatic horticulture, it has since emerged as one of the most problematic invasive aquatic plants in Western Europe, including the Netherlands, where it has had significant ecological, economic, and regulatory impacts.

Introduction and Spread

The species was first observed in the Netherlands in 1994, in a waterway in Rijnsweerd, Utrecht, near the Uithof where the Kromme Rijn connects with surrounding polders (Baas & Holverda, 1996). Though its natural origin is in the Americas, evidence suggests it was likely introduced into Dutch waterways via the aquatic nursery trade. Van der Vlugt is believed to have imported the species from Argentina in 1983, distributing it informally through the Aquatic Plants Working Group, long before it became commercially available in garden centers (Baas & Holverda, 1996).

Favorable climatic conditions, specifically two abnormally warm summers, are believed to have accelerated its establishment and proliferation (Baas & Holverda, 1996). The early growth patterns and spread through Dutch waterways suggest that it primarily disperses through vegetative growth and rhizome displacement via water flow, a characteristic that contributes to its aggressive spread (Djeddour, 2017; Newman & Dawson, 1999).

Ecological and Economic Impact

Following its arrival, the species rapidly became an ecological threat, forming dense, floating mats that covered waterways, blocked light for native macrophytes, reduced oxygen levels, and decreased biodiversity (Djeddour, 2017). Particularly in eutrophic waters, it proved capable of overwintering, especially when protected by existing vegetation, contradicting early expectations that severe winters would limit its survival (Baas & Duistermaat, 1998).

Mechanized removal efforts were initially successful in Utrecht, especially when followed by a cold winter. However, these successes were temporary. In regions like ’s-Hertogenbosch, floating mats reappeared in large volumes, requiring costly removal operations, and the plant eventually spread to the Meuse River and adjacent nature reserves (Baas & Duistermaat, 1998).

In addition to ecosystem degradation, *H. ranunculoides* poses risks to recreational use, water management, and flood control, as its mats can obstruct waterways and infrastructure (Djeddour, 2017; EFSA, 2007).

Methods

Research Design

In this study, a comparative case study methodology is employed in order to analyse the establishment and spread of two invasive plant species: *Rhododendron ponticum* in Ireland and *Hydrocotyle ranunculoides* in the Netherlands. This approach was chosen to allow for context-sensitive analysis of the ecological, biological and anthropogenic factors that contributed to the invasions in each location. The comparison is structured around the MAFIA framework (Pyšek et al., 2020), which takes macroecological variables from three primary categories into account. These are alien species traits, location characteristics and factors related to introduction events.

Framework Application

For each species and location, data was gathered and interpreted under the following components.

1. Alien Species Traits: Reproductive strategy, growth rate, dispersal mechanisms, phenotypic plasticity, and ecological niche breadth.
2. Location Characteristics: Ecosystem structure, native biodiversity, disturbance regimes, climate, land use, and hydrology.
3. Introduction-Related Factors: Propagule pressure, residence time, introduction pathway, socioeconomic drivers, and human facilitation.

Data Collection

This review utilises a qualitative synthesis of peer-reviewed literature, as well as news publications and government or NGO reports. These were obtained using academic databases such as Google Scholar, ScienceDirect and Web of Science. Inclusion criteria included peer-reviewed reports, relevance to invasion biology and the species under study, and publication dates primarily post-2000 with foundational texts included where necessary (e.g., Elton, 1958).

Comparative Analysis

Case studies of each invasive species were independently analysed using the MAFIA framework. This was then used to inform a cross-case comparison.

Results

Case Study: *Rhododendron ponticum*

The factors that lead to the successful invasion of *R. ponticum* have been extensively discussed in the field of invasion biology. This case study applies the MAFIA (Macroecological Framework for Invasive Aliens) framework, as proposed by Pyšek et al. (2020), to examine the factors influencing the establishment and spread of *R. ponticum* in the Ireland, analysing the roles of alien species traits, location characteristics, and introduction-related factors.

Numerous biological-ecological characteristics have been identified as contributors, such as hardiness and ease of propagation (Dehnen-Schmutz & Williamson, 2006; Casati et al., 2022). However, such characteristics tend to be common to the entire *Rhododendron* genus, of which about four to five hundred species are grown as ornamentals in Britain and Ireland (Dehnen-Schmutz & Williamson, 2006). They are not exclusive to *ponticum*; it is therefore evident that human-mediated factors also have played a significant role in its spread. Such factors may include large-scale planting, hybridisation, and destruction of local environments (Erfmeier & Bruelheide, 2009; Dehnen-Schmutz & Williamson, 2006).

Introduction and event related factors

Following its arrival to Great Britain and Ireland via the ornamental trade, *R. ponticum* experienced a rise in popularity due to its visually appealing purple flowers, ease of propagation, use in game cover and use as root stock for other ornamental rhododendrons (Dehnen-Schmutz & Williamson, 2006). It was also extremely affordable, almost always being the cheapest *Rhododendron* species available to buy (Dehnen-Schmutz & Williamson, 2006).

The establishment of *R. ponticum* can therefore be attributed in part to high propagule pressure that resulted from intense periods of planting (Dehnen-Schmutz & Williamson, 2006). Studies from the highly-invaded Killarney Oakwoods show that it was commonly planted around houses, with the densest thickets occurring close to habitations and the individual plants often occurring in regular lines (Cross, 1981). Criticisms of massive plantings were recorded during the 19th century, however data on the dates and sites of planting as well as the dates of spread to unintended habitats are limited, due in part to botanical recording ignoring the presence of ornamentals (Dehnen-Schmutz & Williamson, 2006).

Biological and ecological factors

Following introduction and establishment, there are a number of biological-ecological characteristics that contributed to the invasion of *R. ponticum* (Barron, 2007; Casati et al., 2022). It produces large quantities of small, wind-dispersed seeds, and is shade tolerant (Barron, 2007; Casati et al., 2022). It is avoided by grazers due to the presence of andromeda-toxin in its leaves, which are highly toxic if ingested (Barron, 2007; Casati et al., 2022). If cut back, it resprouts quickly, with cut stumps able to produce multiple shoots of regrowth that are then also more likely to flower more vigorously (Barron, 2007). It can also quickly recolonise a cleared area if seed sources are left behind (Barron, 2007; Casati et al., 2022; Dehnen-Schmutz & Williamson, 2006).

Location factors

Another important factor in the invasive success of *R. ponticum* is the level of disturbance of the habitat it is introduced to (Cross, 1981; Casati et al., 2022). In the Killarney

Oakwoods, for example, disturbance by grazers such as the non-native sitka deer, as well as cattle, sheep and goats have severely impacted the woodlands (Cross, 1981; Dehnen-Schmutz et al., 2006). This has left the herb layer with poor species richness due to overgrazing, while the bryophyte layer remained well developed and rich in species (Cross 1981; Erfmeier & Bruelheide, 2009). This bryophyte layer provides an abundance of safe sites for seedlings of *R. ponticum* (Long & Williams, 2007; Cross, 1981). Further evidence of disturbance being critical to *R. ponticum* regeneration is provided by the number of seedlings which develop in forestry plantations after timber extraction, and the spread of seedlings in sand dune systems of Norfolk after overgrazing by rabbits (Cross, 1981).

Table 1

Application of the MAFIA framework to Rhododendron ponticum in Ireland

MAFIA Category	Key Factors	Summary of Evidence
Alien Species Traits	Shade tolerance, seed and clonal spread	Seeds widely dispersed by wind; forms dense thickets that inhibit native regeneration (Gioria et al., 2023; Kumschick et al., 2015).
	Allelopathy and ecological dominance	Produces phenolic compounds that suppress native flora (Elton, 1958; Blackburn et al., 2011).
Recipient Environment	Acidic soils, woodlands, historical land management	Prefers acidic soils of Irish oak woodlands; early introduction aided by estate plantings (Catford et al., 2022).
	Limited natural resistance	Low biotic resistance due to simplified understory communities (Ackerman et al., 2017).
Introduction Factors	Ornamental introduction and landscape use	Introduced in the 18th century; widespread use in estates and hunting grounds (Pyšek et al., 2020).
	High propagule pressure and long residence time	Multiple introduction events and long-established populations (Cassey et al., 2018; Seebens et al., 2020).

Ecological and economic impacts

R. ponticum invasion has had significant ecological and economic effects in Great Britain and Ireland. It outshades native species, letting only 2% of light through its dense bushes, which leads to the death of herb species and the inability of native species to regenerate (Casati et al., 2022). Bryophytes and lichen diversity declines in areas with large bushes (Long and Williams, 2007). Bird species richness is also negatively impacted (Jones, 1972). Malo et al. (2012) found that *R. ponticum* is associated with an increased abundance of some native mammals, such as wood mice, which increases seed predation and provides ticks with more hosts. Further, the nectar of *R. ponticum's* flowers is toxic to many native pollinators, and the allelochemicals present in its leaf litter lead to lower invertebrate biomass (Tiedeken and Stout 2015; Malo et al., 2012; Cross 1975). It also acts as a reservoir for the fungal pathogen *Phytophthora ramorum*, or sudden oak death, which is itself a species that has been identified as a high-risk invader in Ireland and Northern Ireland (Williams et al., 2010; Kelly et al., 2013).

Described as the most expensive alien plant conservation problem in Britain and Ireland by Dehnen-Schmutz and Williamson (2006), the costs associated with *R. ponticum* are primarily associated with its management and control in forestry (Casati et al., 2022). In their economic analysis of the control efforts being utilised on *R. ponticum* in the British Isles, Dehnen-Schmutz et al. (2003) surveyed a number of landowners and land managers in Britain and Ireland in order to estimate the costs associated with managing this invader. 56 respondents who indicated that they wished to control *R. ponticum* estimated their total costs to come to 17 million pounds per year, which comes to about 2,800 pounds per hectare (Dehnen-Schmutz et al., 2003). The authors further describe that the level of control effort expended by private landowners and managers falls short of the social optimum by more than 100%, which indicates that economic impacts could be exacerbated if action is not taken (Dehnen-Schmutz et al., 2003).

Lessons and recommendations

The case of *R. ponticum* in Ireland provides valuable information about the interactions of biological, location and event-related factors. The application of the MAFIA framework allows for the following insights:

Trait-based predictions concerning invasive behaviour are insufficient on their own. While many *Rhododendron* species share traits, *R. ponticum* became invasive, highlighting the necessity of integrating factors such as propagule pressure and location conditions into risk assessment models.

Human-mediated factors are major drivers of invasion. Historical trends in horticulture, habitat disturbance and land-use change had cumulative effects that drove the spread of *R. ponticum*. These factors tend to be underrepresented in invasion models.

Disturbance amplifies the invasibility of *R. ponticum*. Ecosystems that have been weakened by overgrazing or forestry are particularly at risk. Together, high propagule pressure and high levels of disturbance appear to significantly increase the probability and severity of invasion.

Case Study: *Hydrocotyle ranunculoides*

Hydrocotyle ranunculoides, commonly known as floating pennywort, is an invasive aquatic plant native to North and South America (Baas & Holverda, 1996). Since its introduction to Europe, it has become one of the most aggressive aquatic invaders in the Netherlands. Its rapid vegetative reproduction, capacity for mat formation, and resistance to eradication have made it a significant threat to Dutch aquatic ecosystems (Baas & Duistermaat, 1999). This case study applies the MAFIA (Macroecological Framework for Invasive Aliens) framework, as proposed by Pyšek et al. (2020), to examine the factors influencing the establishment and spread of *H. ranunculoides* in the Netherlands, analysing the roles of alien species traits, location characteristics, and introduction-related factors.

Introduction and event related factors

H. ranunculoides was introduced into Europe through the ornamental plant trade (Baas & Holverda, 1996; Baas & Duistermaat, 1999). It was widely sold for use in garden ponds and aquaria during the 1980s and 1990s (Baas & Holverda, 1996; Baas & Duistermaat, 1999)). According to Hulme et al. (2008), ornamental pathways are among the most common introduction routes for aquatic invasive plants in Europe. The socioeconomic appeal of this species — fast-growing, aesthetically pleasing, and easy to cultivate — contributed to its widespread availability before regulatory controls were established (Baas & Holverda, 1996; Baas & Duistermaat, 1999).

Its initial distribution in the Netherlands was primarily linked to anthropogenic release or escape from cultivation (Baas & Holverda, 1996; Baas & Duistermaat, 1999)). As highlighted by Riera et al. (2024), introduction pathways like this are crucial in shaping the assembly and ecological traits of non-native floras. The Netherlands' dense urban landscape, with a high density of managed water bodies and both public and private gardens, facilitated the transition of *H. ranunculoides* from ornamental to naturalised species.

Propagule pressure is a central determinant of invasion success (Cassey et al., 2018; Blackburn et al., 2011). For *H. ranunculoides*, high propagule pressure arose from frequent intentional and unintentional introductions (EPPO, 2007). The repeated presence of the species in commercial garden centers increased the chance of escape, aligning with the findings of Riera et al. (2024) regarding the centrality of human-mediated dispersal.

Residence time is another important factor. First recorded in the Netherlands in the late 1990's, the species rapidly expanded its range within a decade, establishing dense populations. Longer residence time typically correlates with higher establishment and spread probability (Cassey et al., 2018).

Biological and ecological factors

The biological traits of *H. ranunculoides* significantly contribute to its invasive potential. One study by Gioria et al. (2023) shows that invasive plants often exhibit traits such as high relative growth rate, vegetative reproduction, and efficient resource allocation to shoots and leaves, all of which *H. ranunculoides* displays. It reproduces primarily through fragmentation, enabling small plant fragments to colonise new sites rapidly (Newman & Dawson, 1999). It forms dense floating mats that block light, outcompete native macrophytes, and alter aquatic ecosystems (EPPO 2007; Newman & Dawson, 1999).

Pyšek et al. (2023) further elaborate that high phenotypic plasticity, tolerance to eutrophic conditions, and the ability to reproduce vegetatively are strongly associated with invasion success. *H. ranunculoides* exhibits all of these, thriving in low-flow, high-nutrient environments such as those prevalent in Dutch lowland waterways (Djeddour, 2017).

Additionally, the species' resistance to mechanical and chemical control methods complicates its management (Newman & Dawson, 1999). Cuthbert et al. (2022) argue that management costs often exceed available resources when species are not addressed pre-emptively. This highlights the importance of early identification and control.

Location factors

The Netherlands' physical geography and aquatic infrastructure present a highly invasible environment for *H. ranunculoides*. As Lonsdale (1999) suggests, factors like disturbance, nutrient availability, and habitat connectivity shape habitat invasibility. Dutch waterways are highly modified, nutrient-rich, and well-connected through canals and drainage systems, providing ideal conditions for spread.

Ackerman et al. (2017) and Catford et al. (2022) have emphasised the context dependence of invasions. In the Dutch context, widespread eutrophication due to agricultural runoff, coupled with moderate seasonal temperatures and frequent disturbance from maintenance dredging, creates ideal conditions for colonisation and spread (Djeddour, 2017). Moreover, native biodiversity levels in these disturbed systems may be insufficient to exert biotic resistance.

Another facilitating feature is the low-flow nature of Dutch water bodies. According to Seebens et al. (2020), regions with slower water movement tend to accumulate more invasive aquatic plants due to prolonged residence time of propagules.

Table 2

Application of the MAFIA framework to Hydrocotyle ranunculoides in the Netherlands

MAFIA Category	Key Factors	Summary of Evidence
Alien Species Traits	High vegetative growth and plasticity	Rapid clonal growth, overwintering capability, and regrowth from fragments (Newman & Dawson, 1999; Djeddour, 2017).
	Resistance to control	Resistant to herbivory, mechanical removal, and some herbicides (Djeddour, 2017; Hussner et al., 2019).
Location Characteristics	Eutrophic and disturbed aquatic systems	Thrives in slow-flowing, nutrient-rich canals and rivers; sensitive to frost unless buffered by other vegetation (Baas & Duistermaat, 1999).
	Lack of natural enemies	No specialist herbivores or pathogens in Europe (EFSA, 2007).
Introduction Factors	Horticultural/aquarium trade	Likely introduced by aquatic plant enthusiasts in the 1980s; spread via water networks (Baas & Holverda, 1996).
	Propagule pressure	High, due to multiple plantings and dispersal through canals (Cassey et al., 2018; Catford et al., 2022).

Ecological and economic impacts

The socioeconomic context of the *H. ranunculoides* invasion of the Netherlands further complicates control. Although Dutch waterboards and municipalities now recognise the threat, control efforts are fragmented and reactive rather than coordinated and pre-emptive. According to Cuthbert et al. (2022), such insufficient proactive management is a global issue, often leading to higher long-term costs.

Legislative responses have included the EU Regulation on Invasive Alien Species, which bans the sale and transport of *H. ranunculoides*. However, enforcement remains a challenge. Bellard et al. (2016, 2019) show that alien species continue to drive biodiversity loss despite regulatory frameworks, especially when local implementation is inconsistent.

The ecological impacts of *H. ranunculoides* in the Netherlands are extensive. Its dense mats reduce light availability, altering photosynthetic dynamics and suppressing native macrophyte growth (Newman & Dawson, 1999; Djeddour, 2017). Oxygen levels decline under these mats, leading to anoxic conditions detrimental to fish and invertebrates (Newman & Dawson, 1999; Djeddour, 2017).

Kumschick et al. (2015) quantify ecological impacts of alien species using standardised metrics, placing *H. ranunculoides* in the higher-impact range due to its transformation of habitats. Its ability to clog waterways disrupts recreational and commercial navigation, while also increasing flood risk by obstructing water flow (EPPO, 2007).

From an economic perspective, control and maintenance costs are substantial. Dutch waterboards spend millions annually on mechanical removal and chemical treatment (Millane & Caffrey, 2014). Despite these efforts, reinvasion is common due to incomplete eradication and continued fragmentation. This aligns with findings by Cuthbert et al. (2022), who note that reactive management leads to spiralling costs over time.

Lessons and recommendations

The case of *H. ranunculoides* in the Netherlands offers valuable lessons about the interplay of species traits, local context, and human-mediated introductions. Applying the MAFIA framework highlights the following insights:

Species traits (vegetative reproduction, mat formation, tolerance to eutrophication) are highly conducive to invasion.

Location characteristics (nutrient-rich, connected water systems, disturbed habitats) strongly facilitate spread.

Human factors (propagule pressure via the ornamental trade, lack of early control, inconsistent regulation) have exacerbated the problem. Future management must prioritise early detection and rapid response (EDRR), stricter enforcement of trade restrictions, and coordinated control strategies. Greater investment in public awareness and ecological restoration of water bodies may also increase resilience to invasion.

Comparative Analysis

The following table presents the primary findings of each case study in a comparative manner.

Table 3

Comparative synthesis of the differences and similarities between *H. ranunculoides* and *R. ponticum*

Dimension	*Hydrocotyle ranunculoides* (Netherlands)	*Rhododendron ponticum* (Ireland)
Introduction Pathway	Aquarium/horticultural trade (unintentional escape)	Intentional ornamental planting
Primary Dispersal Mechanism	Vegetative spread via water currents	Wind-dispersed seeds and clonal growth
Habitat Type	Aquatic, eutrophic water bodies	Temperate woodland and heathland
Control Difficulty	High; rapid regrowth from fragments, resistant to chemical and manual control	High; long-lived seed bank, chemical and physical persistence
Policy Response	Recent bans and inclusion on European Union concern list	Long-standing problem, often addressed in invasive plant strategies
Biotic Resistance	Low due to absence of natural enemies	Low due to simplified forest ecosystems
Socioecological Impact	Waterway blockage, biodiversity decline, increased flood risk	Forest degradation, suppression of native understory, loss of biodiversity

Discussion

This discussion will synthesise findings from the application of the MAFIA framework to two case studies: *Rhododendron ponticum* in Ireland and *Hydrocotyle ranunculoides* in Ireland and Great Britain. Each invasion was analysed through the lens of introduction pathways, establishment pathways, ecological impacts and human responses. This macroecological approach allows for the identification of patterns of vulnerability, management gaps and economic consequences that can inform predictive modelling of future biological invasions and invasion research.

Comparative Invasion Dynamics

Both *H. ranunculoides* and *R. ponticum* are prime examples of ornamental introductions that have transitioned into aggressive invaders, primarily as a result of human-mediated factors such as propagule pressure. Despite differences in their habitats (aquatic vs. terrestrial), both species have benefited from a lack of strong biotic resistance in their non-native ranges, as well as ecological flexibility that allowed them to thrive in these disturbed landscapes.

In the Netherlands, *H. ranunculoides* exploited eutrophic, low-flow freshwater systems where native plant competition was weak and physical disturbances rare. Its mat-forming growth pattern and clonal reproductive strategy enabled rapid spread, with establishment driven primarily by human disposal from private ponds and aquaria. In contrast, *R. ponticum* in Ireland and Great Britain took advantage of historical forestry mismanagement and the resulting lack of native herbivory, establishing extensive monocultures across acidic woodlands, moorlands and parklands.

Despite their contextual differences, both species demonstrate the importance of context dependence in invasion success. The strength and relevance of different MAFIA components varied between species. Propagule pressure and control challenges were critical to the invasion of *R. ponticum*, while the invasion of *H. ranunculoides* was primarily driven by anthropogenic disturbance and the hydrological traits of invaded systems.

Ecological Impacts

The ecological effects for both species are substantial, though they manifest differently due to the contrasting qualities of the ecosystems they invade. *H. ranunculoides* disrupts aquatic ecosystems by outcompeting submerged macrophytes, decreasing oxygen levels and impeding water flow. This degrades the native habitat for native invertebrates, plants and fish. In addition, the dense mats it forms reduce recreational and navigational access.

Conversely, *R. ponticum* creates dense, shady thickets in terrestrial ecosystems, which suppress native understory vegetation, alters soil chemistry via alleopathy and reduces invertebrate and bird diversity (Casati et al., 2022; Rotherham, 1983). The result is a homogenised landscape with diminished ecosystem services, particularly in conservation-designated areas such as national parks.

The scale and longevity of *R. ponticum*'s impacts arguably exceed those of *H. ranunculoides*, given its integration into upland forest and moorland ecosystems over the past century. However, the more rapid recent spread of *H. ranunculoides* highlights how aquatic invasions can have acute effects within shorter timescales.

Human Management and Response

In both cases, delayed responses and inconsistent national policies contributed to the expansion of each species. *R. ponticum* was long tolerated and even encouraged in Ireland and Great Britain as a result of its aesthetic and hunting-related value, with widespread recognition of its invasiveness only emerging in the late 20th century. Meanwhile, *H. ranunculoides* continued to be traded in the Netherlands until an EU-wide ban was enacted in 2016.

Where management has occurred, it has been fragmented and reactive. In Ireland and Great Britain, mechanical removal and herbicide application for *R. ponticum* are costly and often followed by regrowth, necessitating long term, resource-intensive efforts. In the Netherlands chemical and manual removal of *H. ranunculoides* faces challenges in the form of accessibility and efficiency due to its aquatic setting and the rapid regeneration of fragmented stolons.

These challenges highlight the importance of incorporating invasion stages into risk assessment frameworks. Both species were most manageable at the pre-establishment stage, but insufficient early regulation driven by lack of awareness, economic incentives and lack of trade restrictions undermined the proactive containment of their spread.

Economic Impact and Projected Costs

Hydrocotyle ranunculoides in the Netherlands

Economic costs of *H. ranunculoides* in the Netherlands are primarily incurred through its impacts on water management structure and navigation, due to the dense floating mats that increase flood risk by clogging drainage systems and weirs (Millane & Caffrey, 2014). Dutch water boards have spent millions on manual removal operations since the early 2010s (Millane & Caffrey., 2014). Estimates from the invasive species cost database InvaCost suggest that *H.*

ranunculoides generated approximately €2.5 to €5 million in direct costs in the Netherlands between 2010 and 2020 (Diagne et al., 2020). Projections based on continued spread and inflation-adjusted labour and chemical control costs suggest this could rise to over €10 million by 2035, particularly under climate warming scenarios that favour aquatic plant growth (Diagne et al., 2020).

Indirect costs such as losses in biodiversity, recreational revenue and fishery impacts remain harder to quantify but are likely substantial. Future economic models should integrate economic service valuation and stakeholder-specific losses to present a fuller picture of the costs of an invasion.

***Rhododendron ponticum* in Ireland and Great Britain**

The economic costs of *R. ponticum* in Ireland and Great Britain are more diffuse but widespread. Unlike *H. ranunculoides*, *R. ponticum*'s terrestrial habitat enables easier logistical planning for removal, but its eradication is more labour and cost intensive over time. Between both countries, an estimated cost of €7.5 to €14 million is incurred annually through combined costs of control and forestry losses (Dehnen-Schmutz & Williamson, 2003). In Ireland alone, annual control efforts are estimated at €1.5–2 million, primarily funded by the National Parks and Wildlife Service (NPWS) and supported by volunteer-led clearance initiatives (Dehnen-Schmutz & Williamson, 2003, Dehnen-Schmutz & Williamson, 2006). Despite decades of investment, high regrowth rates, inaccessible terrain and insufficient long-term follow up have meant that it remains a significant problem (Dehnen-Schmutz & Williamson, 2006).

If current management trends continue, projected cumulative costs may exceed €50–60 million by 2040 (Dehnen-Schmutz & Williamson, 2003). These figures do not account for indirect economic losses due to degraded forest productivity (for example due to *R. ponticum*'s role as a vector for sudden oak death) and opportunity costs of labour and land use. Similarly to *H. ranunculoides* in the Netherlands, these costs need to be better evaluated and incorporated into economic models.

Strategic Comparisons

When comparing the economic impacts of these two species, *R. ponticum* imposes greater cumulative long-term costs due to its integration into upland and conservation-critical landscapes and the difficulty of total removal. In contrast, *H. ranunculoides* incurs more acute, infrastructure-related costs that are locally intense but potentially more contained with efficient early action.

Investment in proactive management, such as monitoring via remote sensing, regulation of plant trade and rapid response funding could substantially reduce future economic burdens. Prevention remains far more cost-effective than long-term control.

Limitations

As a literature-based review, the study is limited by the availability and consistency of existing data. Some ecological or socioeconomic variables (e.g., precise propagule pressure values or disturbance metrics) were not quantifiable across both cases, necessitating qualitative interpretation. Additionally, the retrospective nature of the analysis limits the ability to make experimental inferences; however, the comparative framework allows for robust hypothesis generation and contextual insights.

Implications for Predictive Modelling and Future Invasions

These case studies affirm the value of integrating historical invasion patterns with frameworks like MAFIA to predict future risks. For example, the commercial popularity and dispersal vectors of both species were known well before their widespread establishment. If such data had been systematically used for horizon scanning (Catford et al., 2022), both invasions could have been partially mitigated.

Furthermore, the role of context particularly habitat susceptibility, trade routes, and regulatory gaps must be embedded in predictive models. Data from global databases (e.g., GRIIS, InvaCost) and long-term monitoring platforms can enhance forecasting accuracy if paired with ecological trait data and human activity patterns.

In conclusion, the invasions of *H. ranunculoides* and *R. ponticum* demonstrate how slow political action, inconsistent regulation, and underutilised early warning tools can transform ornamental species into entrenched economic and ecological threats. Embedding these lessons into both national policy and international plant trade regulations will be essential to avoid similar scenarios in the future.

Conclusion

This thesis set out to answer the question: “What ecological and socioeconomic factors have influenced the differential establishment and impact of *Rhododendron ponticum* in Ireland and *Hydrocotyle ranunculoides* in the Netherlands?” By applying the MAFIA framework to two distinct case studies, this research has identified the primary drivers of invasion success that are both species-specific and context-dependent.

The findings show that while both species share traits commonly associated with invasiveness (e.g. high propagule pressure, tolerance to disturbance, and the absence of natural enemies), the environmental and human contexts in which they were introduced played a significant role in their establishment and impact. In Ireland, *R. ponticum* spread rapidly due to favourable soil conditions, a lack of early regulation, and its use in landscaping, resulting in long-term ecological degradation and substantial economic costs. In the Netherlands, *H. ranunculoides* exploited eutrophic, slow-flowing waterways and benefitted from initial availability through the ornamental trade, leading to acute management challenges in aquatic infrastructure and biodiversity conservation.

The comparative analysis reinforces the importance of addressing context dependence in invasion biology. It also emphasises the urgent need for proactive management measures, early detection systems, and policy frameworks that consider not only species traits but also socioeconomic pathways and ecosystem vulnerability.

It is evident that the effectiveness of invasive species management is dependent not only on ecological understanding but also on anticipating how human actions shape invasion dynamics. Historical invasion data, when analysed through structured frameworks like MAFIA, can inform more predictive and preventative strategies across diverse contexts.

Bibliography

Ackerman, J. D., Tremblay, R. L., Rojas-Sandoval, J., & others. (2017). Biotic resistance in the tropics: Patterns of seed plant invasions within an island. *Biological Invasions*, 19, 315–328. https://doi.org/10.1007/s10530-016-1281-4

Alpert, P., Bone, E., & Holzapfel, C. (2000). Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics, 3*(1), 52–66. https://doi.org/10.1078/1433-8319-00004

Baas, W. J., & Duistermaat, L. H. (1999). De opmars van Grote waternavel (*Hydrocotyle ranunculoides* L.f.) in Nederland, 1996–1998. *Gorteria Dutch Botanical Archives, 25*(4), 77–82.

Baas, W. J., & Holverda, W. (1996). Hydrocotyle ranunculoides L.f. (Grote waternavel): de stand van zaken. *Gorteria: tijdschrift voor de floristiek, de plantenoecologie en het vegetatie-onderzoek van Nederland*, *22*(6), 164–165.

Baker, B. G., Bedford, J., & Kanitkar, S. (2017). Keeping pace with the media; Giant Hogweed burns—A case series and comprehensive review. *Burns*, 43(5), 933–938. https://doi.org/10.1016/j.burns.2016.10.018

Barron, C. 2007. The Control of Rhododendron in Native Woodlands. In: LITTLE, D. (ed.) Native Woodland Scheme Information Note No. 3. Forest Service: Woodlands of Ireland Coillearnacha.

Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, 12, 20150623. https://doi.org/10.1098/rsbl.2015.0623

Benedict, M. Q., Levine, R. S., Hawley, W. A., & Lounibos, L. P. (2007). Spread of the tiger: Global risk of invasion by the mosquito Aedes albopictus. *Vector-Borne and Zoonotic Diseases*, 7(1), 76–85. https://doi.org/10.1089/vbz.2006.0562

Blackburn, T. M., Bellard, C., & Ricciardi, A. (2019). Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment*, 17(5), 203–207. https://doi.org/10.1002/fee.2020

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, 26(7), 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Briski, E., Chan, F. T., Darling, J. A., Lauringson, V., MacIsaac, H. J., Zhan, A., & Bailey, S. A. (2018). Beyond propagule pressure: importance of selection during the transport stage of biological invasions. *Frontiers in ecology and the environment*, 16(6), 345–353. https://doi.org/10.1002/fee.1820

Casati, M., Kichey, T., & Decocq, G. (2022). Monographs on invasive plants in Europe: Rhododendron ponticum L. Botany Letters. https://doi.org/10.1080/23818107.2022.2052182

Casati, M., Kichey, T., Closset, D., Spicher, F., & Decocq, G. (2023). Is the invasive Rhododendron ponticum L. an emergent threat to mainland Atlantic forests? A population dynamics approach. *Forest Ecology and Management*, 549, 121463. https://doi.org/10.1016/j.foreco.2023.121463

Cassey, P., Delean, S., Lockwood, J. L., Sadowski, J. S., & Blackburn, T. M. (2018). Dissecting the null model for biological invasions: A meta-analysis of the propagule pressure effect. PLOS Biology, 16(4), e2005987. https://doi.org/10.1371/journal.pbio.2005987

Catford, J.A., Jansson, R. and Nilsson, C. (2009), Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, 15: 22-40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Catford, J. A., Wilson, J. R. U., Pyšek, P., Hulme, P. E., & Duncan, R. P. (2022). Addressing context dependence in ecology. *Trends in Ecology & Evolution*, 37(2), 158–170. https://doi.org/10.1016/j.tree.2021.10.006

Cross, J. R. (1975). Rhododendron Ponticum L. *Journal of Ecology*, *63*(1), 345–364. https://doi.org/10.2307/2258859

Cross, J. R. (1981). The Establishment of Rhododendron Ponticum in the Killarney Oakwoods, S. W. Ireland. *Journal of Ecology*, *69*(3), 807–824. https://doi.org/10.2307/2259638

Cuthbert, R. N., Diagne, C., Hudgins, E. J., Turbelin, A., Ahmed, D. A., Albert, C., Bodey, T. W., Briski, E., Essl, F., Haubrock, P. J., Gozlan, R. E., Kirichenko, N., Kourantidou, M., Kramer, A. M., & Courchamp, F. (2022). Biological invasion costs reveal insufficient proactive management worldwide. *Science of The Total Environment,* 819, 153404. https://doi.org/10.1016/j.scitotenv.2022.153404

Dehnen-Schmutz, K., & Williamson, M. (2006). Rhododendron ponticum in Britain and Ireland: Social, economic and ecological factors in its successful invasion. *Environment and History*, 12(3), 325–350. https://www.jstor.org/stable/20723582

Diagne, C., Leroy, B., Gozlan, R. E., Vaissière, A.-C., Assailly, C., Nuninger, L., … Courchamp, F. (2020). *InvaCost: Economic cost estimates associated with biological invasions worldwide* (Version 5) [Dataset]. Figshare. https://doi.org/10.6084/m9.figshare.12668570.v5

Djeddour, D. (2017). Hydrocotyle ranunculoides (floating pennywort). In CABI Compendium. https://doi.org/10.1079/cabicompendium.28068

Elton, C. S. (1958). The ecology of invasions by animals and plants. Methuen.

European Food Safety Authority (EFSA). (2007). Opinion of the Scientific Panel on Plant Health on the pest risk analysis made by EPPO on Hydrocotyle ranunculoides L. f. (floating pennywort). *EFSA Journal*, 5(9), 468. https://doi.org/10.2903/j.efsa.2007.468

Gioria, M., Hulme, P. E., Richardson, D. M., & Pyšek, P. (2023). Why are invasive plants successful? *Annual Review of Plant Biology*, 74, 635–670. https://doi.org/10.1146/annurev-arplant-070522-071021

Hayes, K. R., & Barry, S. C. (2008). Are there any consistent predictors of invasion success? *Biological Invasions, 10*, 483–506. https://doi.org/10.1007/s10530-007-9146-5

Higgins, T., Lower, C., & Killarney, C. K. (2005). Managing the threat of invasive plant species to Ireland's native woodlands. In Ireland's Native Woodlands: Conference Proceedings Galway 8–11 September 2004 (p. 2).

Hughes, K. (2015, February 28). Plant fight cost €2.8m in a decade. Irish Independent. https://www.independent.ie/regionals/kerry/news/plant-fight-cost-28m-in-a-decade/31019768.html

Hui, C., Richardson, D. M., Robertson, M. P., Wilson, J. R., & Yates, C. J. (2011). Macroecology meets invasion ecology: linking the native distributions of Australian acacias to invasiveness. *Diversity and distributions*, 17(5), 872-883.

Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pyšek, P., Roques, A., Sol, D., Solarz, W., & Vilà, M. (2008). Grasping at the routes of biological invasions: A framework for integrating pathways into policy. Journal of *Applied Ecology*, 45(2), 403–414. https://doi.org/10.1111/j.1365-2664.2007.01442.x

Hussner, A., Denys, L., & van Valkenburg, J. (2012). Hydrocotyle ranunculoides. NOBANIS – Invasive alien species fact sheet.

Jeschke, J. M., Gómez Aparicio, L., Haider, S., Heger, T., Lortie, C. J., Pyšek, P., & Strayer, D. L. (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota, 14*, 1–20. https://doi.org/10.3897/neobiota.14.3435

Jones, P. H. (1972). Succession in breeding bird populations of sample Welsh oakwoods. *British Birds, 65*, 299.

Keller, R. P., Geist, J., Jeschke, J. M., & Kühn, I. (2011). Invasive species in Europe: Ecology, status, and policy. *Environmental Sciences Europe*, 23, 23. https://doi.org/10.1186/2190-4715-23-23

Kelly, J., O’Flynn, C., & Maguire, C. (2013). Risk analysis and prioritisation for invasive and non-native species in Ireland and Northern Ireland [Report]. Northern Ireland Environment Agency & National Parks and Wildlife Service, as part of Invasive Species Ireland.

Kikvidze, Z., Suzuki, M., & Brooker, R. (2011). Importance versus intensity of ecological effects: Why context matters. *Trends in Ecology & Evolution, 26*(8), 383–388. https://doi.org/10.1016/j.tree.2011.04.003

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J. M., Pyšek, P., ... & Winter, M. (2015). Ecological impacts of alien species: Quantification, scope, caveats, and recommendations. *BioScience*, 65(1), 55–63. https://doi.org/10.1093/biosci/biu193

Li, Y., & Yu, F.-H. (2023). Managing the risk of biological invasions. *iScience*, 26(11), 108221. https://doi.org/10.1016/j.isci.2023.108221

Litt, A. R., & Pearson, D. E. (2022). A functional ecology framework for understanding and predicting animal responses to plant invasion. *Biological Invasions, 24*, 2693–2705. https://doi.org/10.1007/s10530-022-02813-7

Long, D., & Williams, J. (2007). *Rhododendron ponticum: Impact on lower plants and fungi communities on the west coast of Scotland. Working towards protecting internationally important bryophyte and lichen communities from Rhododendron ponticum invasion* (Scottish Natural Heritage Project No. 19412).

Lonsdale, W. M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80(5), 1522–1536. https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2

Malo, A. F., Godsall, B., Prebble, C., Grange, Z., McCandless, S., Taylor, A., & Coulson, T. (2012). Positive effects of an invasive shrub on aggregation and abundance of a native small rodent. *Behavioral Ecology*, 24(3), 759–767. https://doi.org/10.1093/beheco/ars202

Millane, M., & Caffrey, J. (2014). Risk assessment of Hydrocotyle ranunculoides. Inland Fisheries Ireland.

Ministerie van Landbouw, Natuur en Voedselkwaliteit. (2024). Grote waternavel Hydrocotyle ranunculoides [Fact sheet]. Nederlandse Voedsel- en Warenautoriteit. https://www.nvwa.nl/documenten/plant/planten-in-de-natuur/exoten/risicobeoordelingen/factsheet-grote-waternavel

Nijs, I., Verlinden, M., Meerts, P., Dassonville, N., Domken, S., Triest, L., Stiers, I., Mahy, G., Saad, L., Jacquemart, A.-L., & Cawoy, V. (2012). Biodiversity impacts of highly invasive alien plants: Mechanisms, enhancing factors and risk assessment. Belgian Science Policy – Science for a Sustainable Development Programme.

Ogden, N. H., Wilson, J. R. U., Richardson, D. M., Hui, C., Davies, S. J., Kumschick, S., Le Roux, J. J., Measey, J., Saul, W.-C., & Pulliam, J. R. C. (2019). Emerging infectious diseases and biological invasions: A call for a One Health collaboration in science and management. *Royal Society Open Science, 6*, 181577. https://doi.org/10.1098/rsos.181577

Pyšek, P., Bacher, S., Kühn, I., Novoa, A., Catford, J. A., Hulme, P. E., Pergl, J., Richardson, D. M., Wilson, J. R. U., & Blackburn, T. M. (2020). MAcroecological Framework for Invasive Aliens (MAFIA): Disentangling large-scale context dependence in biological invasions. *NeoBiota*, 62, 407–461. https://doi.org/10.3897/neobiota.62.52787

Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., Tichý, L., Danihelka, J., Chrtek, J., & Sádlo, J. (2009). The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions,* 15(5), 891–903. https://doi.org/10.1111/j.1472-4642.2009.00602.x

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological monographs*, *83*(3), 263-282.

Richardson, D. M., Carruthers, J., Hui, C., Impson, F. A. C., Miller, J. T., Robertson, M. P., ... & Wilson, J. R. U. (2011). Human‐mediated introductions of Australian acacias: A global experiment in biogeography. *Diversity and Distributions,* 17(5), 771–787. https://doi.org/10.1111/j.1472-4642.2011.00779.x

Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions*, 6(2), 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Riera, M., Pino, J., Sáez, L., & Pauchard, A. (2024). Effect of introduction pathways on the invasion success of non-native plants along environmental gradients. *Biological Invasions*, 26, 1561–1580. https://doi.org/10.1007/s10530-024-03270-0

Seebens, H., Bacher, S., Blackburn, T. M., Capinha, C., Dawson, W., Dullinger, S., Genovesi, P., Hulme, P. E., van Kleunen, M., Kühn, I., & others. (2020). Projecting the continental accumulation of alien species through to 2050. *Global Change Biology*, 27, 970–982. https://doi.org/10.1111/gcb.15333

Sih, A., Stamps, J., Yang, L. H., McElreath, R., & Ramenofsky, M. (2010). Behavior as a key component of integrative biology in a human-altered world. *Integrative and comparative biology*, *50*(6), 934-944.

Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human‐induced rapid environmental change. *Evolutionary applications*, 4(2), 367-387.

Stiers, I., Crohain, N., Josens, G., & Triest, L. (2011). Impact of three aquatic invasive species on native plants and macroinvertebrates in temperate ponds. Biological Invasions, 13(12), 2715–2726. https://doi.org/10.1007/s10530-011-9942-9

Tyler, C., Pullin, A. S., & Stewart, G. B. (2006). Effectiveness of management interventions to control invasion by Rhododendron ponticum. Environmental Management, 37(4), 513–522. https://doi.org/10.1007/s00267-005-0127-0

Williams, F., Eschen, R., Harris, A., Djeddour, D., Pratt, C., Shaw, R. S., Varia, S., Lamontagne-Godwin, J., Thomas, S. E., & Murphy, S. T. (2010). The economic cost of invasive non-native species on Great Britain (CABI Project No. VM10066) [Technical report]. CABI.