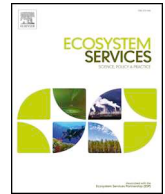




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Linking traits of invasive plants with ecosystem services and disservices

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ABSTRACT

Invasive alien species (IAS) have negative as well as positive effects on human well-being. They can alter ecosystem properties, functions and associated ecosystem services (ES). However, many IAS have negative effects (resulting from reducing ES or by increasing or creating ecosystem disservices (EDS), the latter termed genuine negative effects) on, e.g. biodiversity, crop and timber production and/or human health. We present a novel framework, linking traits of IAS via ES and EDS to affected environmental and socioeconomic sectors. By applying the framework, we were able to identify whether a plant trait affects different sectors (positively and/or negatively) and whether the same trait impacts one but benefits another sector. Positive effects correspond to an increase in ES/a reduction in EDS whereas impact represents a reduction in ES/an increase in EDS. The framework is applicable across traits and species, including the direction (positive/negative) and strength of effects. Furthermore, we classified six socioeconomic and environmental sectors frequently affected (positively or negatively) by invasive plants, along with the list of ES and EDS relevant in these sectors. The framework can be used as a tool for assessing multiple ES and EDS and for prioritizing the management of affected sectors.

1. Introduction

Alien plant species have been introduced by humans all over the globe and many of them have become invasive (i.e. causing impact; see below). They have modified ecosystems for centuries with great effects on the environment and human well-being (Vilà et al., 2010, Vilà and Hulme, 2017). Alien species numbers have increased with the development of agriculture, forestry, and industry (van Kleunen et al., 2015, Pyšek et al., 2017) and this increase is not yet saturated (Seebens et al., 2017). Alien species were reported to have a great effect on agriculture, for instance, in the US introduced species make up 98% of food consumed (Pimentel et al., 2005). Similarly, plant species used in forestry or horticulture are often introduced, e.g. a study in the US showed that 82% of tree species (out of 235) were introduced for landscaping, already in the 17th century, when the first ornamental garden was founded (Reichard and White, 2001). At the same time, there are hundreds of alien woody species (most commonly of the genera *Pinus*, *Eucalyptus* and *Acacia*) commercially planted for timber (Holmes et al., 2009). Herbaceous plant species are introduced as ornamentals in botanical gardens or private gardens because of their exotic appearance (Hulme et al., 2018, van Kleunen et al., 2018) or for the production of

pharmaceutical and cosmetic compounds (Scott, 2010). In Europe, the majority of alien plant species were introduced for agriculture, forestry, materials, horticulture or as ornamental species (Lambdon et al., 2008). Further, alien species are used in ecosystem restoration, for soil stabilization, and as phytoremediators or windbreakers (Pejchar and Mooney, 2009).

While ecosystem services (ES) present direct or indirect positive effects, disservices (EDS) generate functions, processes and attributes in ecosystems that result in perceived or actual negative impacts on human well-being (Shackleton et al., 2016). We extend this notion to encompass biodiversity, as well. In this paper, we first introduce invasive alien plant species and their environmental and socioeconomic effects. Further, we present plant functional traits linked with invasiveness and ES/EDS. Additionally, we overviewed main ES/EDS of invasive plant species in Europe as a rationale for a conceptual framework that links IAS, traits and ES/EDS. Here, we used the Common International Classification of Ecosystem Services (CICES; Haines-Young and Potschin, 2012) where ES can be classified as follows: (i) provisioning services (including food, fiber, pharmaceuticals, water and others); (ii) regulation and maintenance services (climate, water and erosion regulation, nutrient cycling, pollination etc.); and (iii) cultural

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services (spiritual and aesthetic values as well as providing foundation for tourism and recreation development).

2. Background

2.1. Invasive plant species

By now, 13,168 alien plant species have been reported as naturalized around the world (GloNAF – Global Naturalized Alien Floras; van Kleunen et al., 2015, Pyšek et al., 2017, van Kleunen et al., 2019), with highest numbers in North America (5958 taxa), Europe (4139) and Australasia (3886; Pyšek et al., 2017). Alien species that successfully naturalize in a new area (i.e. forming self-sustaining populations by reproducing in the wild without human intervention and thus become permanent parts of the flora; Richardson et al., 2000, Pyšek et al., 2012a), do not necessarily modify their new habitat or cause positive or negative effect on environment or people. Vilà et al. (2010) showed that 5–6 percent of alien plant species in Europe are noted to have an environmental and socioeconomic effect. Estimates of the total numbers of invasive plant species over the globe vary (e.g. 451 in Weber (2003), excluding agricultural weeds, or 672 in the CABI Invasive Species Compendium; www.cabi.org/isc).

In this paper, we term these “invasive alien species” (IAS), following the IUCN (2000) definition rather than the one commonly used in ecological literature where the criterion for a species to be invasive is rapid spread (Richardson et al., 2000). Therefore, “invasive alien species (IAS) are animals, plants or other organisms that are introduced into places outside their natural range, negatively impacting native biodiversity, ecosystem services or human well-being” (IUCN, 2000). Invasive species are easily transported by people and disperse effectively (Wilson et al., 2016). Additionally, they can rapidly adapt to a range of environmental conditions and therefore, inhabit a variety of ecosystems (Hellmann et al., 2008).

2.2. Environmental and socioeconomic effects of IAS

Invasive plant species have negative impacts on the environment, public health, recreation or infrastructure (Pyšek et al., 2012b, Blackburn et al., 2014, Jeschke et al., 2014), related to reduced provision of ES or increased EDS (Vaz et al., 2017, Potgieter et al., 2019). The most frequently documented impacts of invasive species on ecosystems are competition for resources with other plant species (Kumschick et al., 2015) and the spread of diseases and pests (Pimentel et al. 2005, Holmes et al. 2009). Many studies have shown that invasive species impact the diversity of native species in invaded plant communities (Hooper et al., 2005, Hejda et al., 2009, Pyšek et al., 2012b). Biodiversity has an important role in supporting ecosystem functioning and ecosystem services (e.g. food provision, nutrient cycling, microclimate regulation; Altieri, 1999) and according to Millennium Ecosystem Assessment (2005) the maintenance of biodiversity provides significant benefits to humans (although not every ES directly depends on biodiversity; Schwarz et al., 2017). Still, biodiversity is also an important asset (and hence service) in itself. Furthermore, invasive plants can have detrimental effects on ecosystems by altering nutrient and water cycles or facilitating erosion (Kettunen et al., 2008).

Agriculture, forestry and tourism can profit from IAS, however economic costs of losses, damage and control can exceed the profits they provide (Pimentel et al., 2005). For example, in the US, IAS cause the major losses in crop production resulting in 26.4 billion dollar loss per year, including a loss of 21 billion dollars by introduced pests and microbes (Pimentel et al., 2005). Similarly, invasive pathogens result in considerable losses in forestry and recreation sectors – up to 20.3 and 2 billion US dollars annually, respectively (Pimentel et al., 2005, Holmes et al., 2009). Furthermore, there are additional economic and environmental costs resulting from eradication, such as ecosystem recovery from the damages caused by herbicides or other weed removal

techniques (Pimentel et al., 2005). In the UK, Japanese knotweed (*Fallopia japonica*) causes significant damages to infrastructure (roads, households, railways), with the costs of vegetation management and eradication totaling 165 million pounds, annually (Williams et al., 2010). Finally, IAS can decrease landscape quality and cause health problems (Kettunen et al., 2008, Pyšek and Richardson, 2010, Sladonja et al., 2015, Lazzaro et al., 2018). Overall, in Europe, terrestrial invasive plants cost 3.74 million euros annually, a third of total economic costs caused by all IAS in Europe (Kettunen et al., 2008).

Nevertheless, some IAS can also have beneficial effects, manifested as increased provision of ES or reduced EDS. They can, consequently, affect environmental and socioeconomic sectors (agriculture, forestry, infrastructure, human health, aesthetics and recreation, environmental effect: sectors adapted from categories by Kumschick et al., 2012) positively and negatively (Table 1). For example, some plant invaders, such as *Ailanthus altissima*, can cause severe allergies in humans, yet, the species is used in the pharmaceutical industry due to its beneficial chemical compounds (Sladonja et al., 2015). Ornamental species can increase the recreational value of the landscape but also have an adverse effect on ecosystems by degrading habitats, reducing biodiversity, causing injuries, and being toxic to humans (Potgieter et al., 2017). Invasive tree species used for timber production can at the same time release chemical compounds via allelopathy (Holmes et al., 2009) thereby inhibiting the growth of surrounding trees (decrease in ES). Many ornamental broad-leaved trees emit biogenic volatile organic compounds, which increase the concentration of ozone and photochemical smog in the atmosphere (Niinemets and Peñuelas, 2008). The complexity of ecosystems and interactions between invasive and native species makes identifying the real effects of invasive species difficult.

2.3. Plant traits associated with invasiveness

Many studies showed that certain functional traits of introduced plant species are associated with their ability to become invasive (e.g. flowering period, clonality, height; Pyšek et al., 2015, Pyšek et al., 2009, van Kleunen et al., 2010). In our paper, we consider functional traits as “any trait which impacts fitness indirectly via its effects on growth, reproduction and survival” (Violle et al., 2007). Some traits associated with plant invasiveness include: growth rate (IAS grow faster compared with native species), SLA (higher specific leaf area in IAS), flowering phenology (IAS start flowering earlier and have longer flowering periods), higher fecundity and more efficient seed dispersal (Pyšek and Richardson, 2007). Given the relationship of plant traits with plants’ invasiveness we argue that plant traits can be an important tool for predicting benefits (ES) or impacts (EDS) for different environmental and socioeconomic sectors (Table 1): Traits do affect ecosystem functions (Díaz et al., 2004), which humans might perceive as services or disservices that can translate into societal (monetary or non-monetary) values (cf. ecosystem service cascade; Haines-Young et al., 2010).

Thus, it is important to make a distinction (Fig. 1) between response and effect traits (Lavorel and Garnier, 2002) in different stages of the invasion process, i.e. transport and introduction to a new area, establishment of self-sustaining populations (naturalization), and spread within the new area (Richardson et al., 2000).

Response traits respond to environmental changes (e.g. life form, SLA, life cycle, relative growth rate, leaf and root morphology and seed mass; Lavorel and Garnier, 2002). Therefore, they are crucial throughout the invasion process, predominantly during the plants’ establishment and spread phases when plants need to overcome environmental barriers (Richardson et al., 2000). Different traits may be beneficial in different phases of the invasion process (Richardson and Pyšek, 2012) – such as ornamental traits that might decide which species are transported across countries at all (Reichard and White, 2001). When IAS start to have an impact on ecosystems or economies, effect traits become more relevant since they affect ecosystem

Table 1

List of effects on ecosystem services (increase and reduction in ES) and disservices (increase and reduction in EDS) by invasive plant species in Europe – (+): Increase in ES or EDS; (–): Decrease in ES or EDS.

IAS	Ecosystem service	Ecosystem disservice	References
<i>Acacia dealbata</i>	Used for timber (+); Erosion control (+); Windbreak (+); Ornamental (+); Enhancing pollination (+); Use in cosmetics (+);	Allelopathy (+); Erosion (+); Allergies (+); Nutrient alteration in soil (+);	Lorenzo et al. 2008; Weber, 2003; Lorenzoni-Chiesura et al. 2000; Chau et al. 1985; Logan, 1987; Le Maitre et al. 2011; Clemson, 1985; Griffin et al. 2011;
<i>Ailanthus altissima</i>	Pesticide (+); Use in medicine (+); Used for timber and fuel (+); Ornamental (+); Erosion control (+); Soil stabilization (+); Animal food (+);	Allelopathy (+); Allergies (+); Habitat alteration (+); Infrastructure damage (+);	Gómez-Aparicio & Canham, 2008; Ding et al. 2005; Ballero et al. 2003; Castro-Díez et al. 2009; Grapow & Blasi, 1998; Sladonja et al. 2015; Kowarik & Säumel, 2007; Lee et al. 1997; Heisey, 1997;
<i>Ambrosia artemisiifolia</i>	Crop yield (–); Animal food (+); Use in medicine (+); Phytoremediation (+); Biodiversity (–);	Pest transmission in crops (+);	Reinhardt et al. 2003; Bohár & Kiss, 1999; Beres et al. 2002; Dechamp, 1999; Stubbendieck et al. 1995; Bassett & Crompton, 1975;
<i>Campylopus introflexus</i> <i>Carpobrotus edulis</i>	Ornamental (+); Biodiversity (–); Ornamental (+); Soil stabilization (+); Use in traditional medicine (+); Used as food (+); Biodiversity (–);	Habitat alteration (+); Habitat alteration (+);	Biermann & Daniels, 1997; Daniëls et al. 2008; Weber, 2017; Moretti, 1939; Ordway et al. 2003; van der Watt & Pretorius, 2001;
<i>Cortaderia selloana</i>	Ornamental (+); Erosion control (+); Soil stabilization (+); Biodiversity (–);	Habitat alteration (+); Allergies and injuries (+); Causes fire (+);	Bossard, 2000; DAISIE, 2009; Domènech & Vilà, 2006; Okada et al. 2007;
<i>Echinocystis lobata</i>	Ornamental (+); Use in medicine (+); Biodiversity (–);	Toxic (+);	Ielciu et al. 2017; DAISIE, 2009;
<i>Fallopia japonica</i>	Animal food (+); Use in medicine (+); Pesticide (+); Biofuel (+); Ornamental (+); Biodiversity (–);	Infrastructure damage (+); Floods (+); Allelopathy (+); Habitat alteration (+); Erosion (+);	Palmer, 1990; Beerling et al. 1995; Aguilera et al. 2010; DAISIE, 2009; Seiger & Merchant, 1997; Shaw et al. 2011;
<i>Hedychium gardnerianum</i>	Recreation (–); Ornamental (+); Use in medicine (+); Biodiversity (–);	Recreation (–); Ornamental (+);	Macdonald et al. 1991; Weyerstahl et al. 1998; Minden et al. 2010;
<i>Heracleum mantegazzianum</i>	Recreation (–); Ornamental (+); Use in medicine (+); Used as food (+); Herbicide (+); Biodiversity (–);	Allergies (+); Pathogen transmission (+); Habitat alteration (+); Erosion (+); Allelopathy (+);	Tiley et al. 1996; Jandová et al. 2014; Thiele & Otte, 2007; Wille et al. 2013; Nielsen et al. 2007; Chan et al. 2011; Solymosi, 1994; Westbrooks, 1991; Pyšek, 1991;
<i>Impatiens glandulifera</i>	Recreation (–); Biodiversity (–); Animal food (+); Ornamental (+);	Habitat alteration (+); Erosion (+);	Pattison et al. 2016; Hulme & Bremner, 2006; Beerling & Perrins, 1993; Pyšek & Prach, 1995;
<i>Opuntia ficus-indica</i>	Recreation (–); Biodiversity (–); Ornamental (+);	Injuries (+); Toxic for people and cattle (+);	Larsson, 2004; Brodin, 2004; Nikodinoska et al. 2014; Griffith, 2004;
<i>Oxalis pes-caprae</i>	Honey production (+); Crop yields (–); Tourism (+); Pollinators (+); Biodiversity (–);	Toxic (+);	Marshall, 1987; McLaughlan et al. 2014; DAISIE, 2009;
<i>Paspalum paspaloides</i>	Crop yields (–); Preventing floods (+); Animal food (+); Erosion control (+); Phytoremediation (+); Biodiversity (–);	Attractive for mosquitos/disease transmitters (+);	Holm et al. 1979; Lawler et al. 2007; Bernez et al. 2005; Bor, 1960; Rosicky et al. 2006; Shu et al. 2002; Lee et al. 2004;
<i>Prunus serotina</i>	Forestry (–); Agriculture (–); Ornamental (+); Erosion control (+); Used for timber (+); Used as food (+); Biodiversity (–);	Toxic (+); Soil alteration (+);	Verheyen et al. 2007; DAISIE, 2009; Starfinger et al. 2003; Fowells, 1965; Stephens, 1980;
<i>Rhododendron ponticum</i>	Forestry (–); Pollination (–); Recreation (–); Ornamental (+); Use in medicine (+); Biodiversity (–);	Toxic (+);	Black, 1991; Colak et al. 1998; Milne & Abbott, 2000; Dehnen-Schmutz et al. 2004; Erdemoglu et al. 2003;
<i>Robinia pseudoacacia</i>	Used as biofuel (+); Forestry (+); Ornamental (+); Pollination (+); Used as food (+); Used in cosmetics (+); Biodiversity (–);	Habitat alteration (+); Toxic (+); Infrastructure damage (+);	Sabo, 2000; Benesperi et al. 2012; Rédei et al. 2008; DAISIE, 2009; Rédei et al. 2002; Keresztesi, 1977; Grollier et al. 1986;
<i>Rosa rugosa</i>	Biodiversity (–); Recreation (–); Tourism (+); Erosion control (+); Ornamental (+); Used as food (+); Use in medicine (+); Used in cosmetics (+); Windbreak (+);	Injuries (+); Habitat alteration (+); Pest host/transfer (+);	Vanderhoeven et al. 2005; Isermann, 2008; Shorthouse, 1987; Jørgensen & Köllmann, 2009; Weidema, 2006; Dobson et al. 1990; Dubey et al. 2010; Bruun, 2006;

functioning and the provision of ES or EDS. These include, among others, plant height and biomass (competitive ability), phenology, mutualism with nitrogen-fixing bacteria, longevity, leaf litter quality or photosynthesis pathway (for example, in South Africa most of the invasive grass species are C3 and can have an advantage over C4 species in disturbed ecosystems or with an increase of CO₂, e.g. more efficient nitrogen use in grasses; Milton, 2004).

2.4. Plant traits and ES & EDS

Plants' effects on ES (such as crop yields, cultural services, pollination) are manifested by changing ecosystem functions and related values through the agency of functional traits such as biomass, plant height, canopy and root size/architecture, leaf dry matter content, SLA, soil organic carbon, flowering pattern or leaf P/N concentration (de

Bello et al., 2010; Lavorel et al., 2011). Based on the frequency of certain traits, ecosystems may become "hot-spots" of ecosystem services, fostering multiple services provided by some species (Potgieter et al., 2017), or they can exhibit trade-offs between services and disservices as a result of contrasting traits. Some tree species, due to their fast growth contribute to carbon sequestration, climate regulation or erosion control (ES), while this trait can lead to increase in fire risk (EDS; Castro-Díez et al., 2019). For example, Millward and Sabir (2011) showed that the effect of maple (*Acer platanoides*) on air quality is two-fold; it sequesters carbon dioxide from the air while emitting biogenic volatile organic compounds, which significantly reduce air quality. Such trade-offs can be expressed as a conflict between service and disservice.

In summary, the extent and direction of IAS' effects on ES and EDS can be ambiguous. Thus, it is necessary to create a framework that

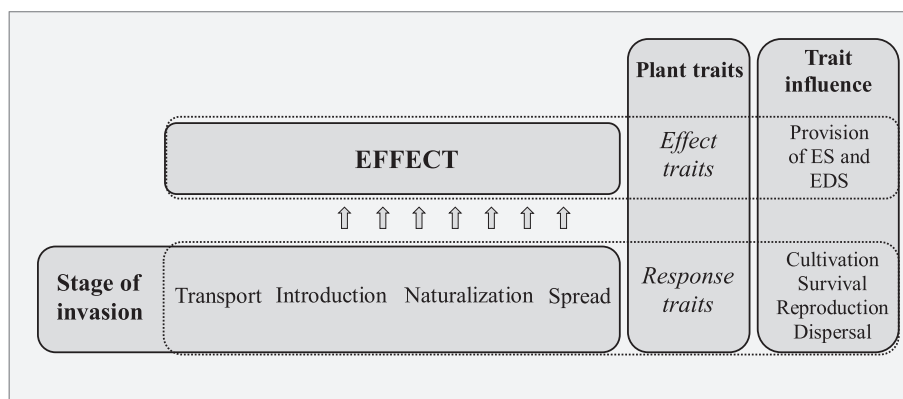


Fig. 1. Different types of plant traits are important for each stage of invasion; response traits in early stages, while effect traits become more significant when introduced species begin to have an impact. However, the effect can be realized at any stage of the process.

provides information on which plant species should be prioritized for management actions in which environmental or socioeconomic sectors, depending on their traits and thus their positive and negative effects. Our paper provides a framework which extends existing ones (e.g. Vaz et al., 2017). It examines the relationship of (functional) traits of invasive plants with ecosystem services and disservices, by linking those traits to affected sectors (agriculture, forestry, infrastructure, human health, aesthetics and recreation, and environmental effect).

Hence, in the proposed paper we aim to (1) identify the main ES/EDS for a variety of invasive plant species; (2) establish the relationship between functional plant traits with increases or decreases in services and disservices; (3) link these traits to different socioeconomic and environmental sectors and highlight those severely affected by invasive plants.

3. Main ES and EDS provided by invasive plant species in Europe

In order to identify the benefits (increase in ES/ decrease in EDS) and impacts (increase in EDS/ decrease in ES) of invasive plant species (Table 1), we chose 18 vascular plant species from the list of

representative invasive species in Europe provided by DAISIE (2009) and surveyed the literature for information on how these species affect ES/EDS. The main aim was to get an overview of ES and EDS provided by the selected invasive plant species in Europe. The main criterion for a species to be included on the DAISIE list was, besides it being classified as invasive in Europe, to cover a range of representative taxa and their impacts (Pyšek and Richardson, 2012), which makes the selection suitable for the purpose of our study. We listed the ES and EDS mentioned in the investigated literature with the direction of their effects (positive or negative; Table 1). For example, for *Fallopia japonica*, the ES reported are the provision of animal food, use in medicine, use as a pesticide and biofuel, and ornamental value (Table 1). However, *F. japonica* negatively affects infrastructure, can cause floods (thick plant shoots can block water flow; Palmer 1990, Colleran and Goodall, 2014), produces allelopathic chemicals and changes of habitat (Murrell et al., 2011).

4. Conceptual framework

We propose a novel framework (Fig. 2) linking invasive plant

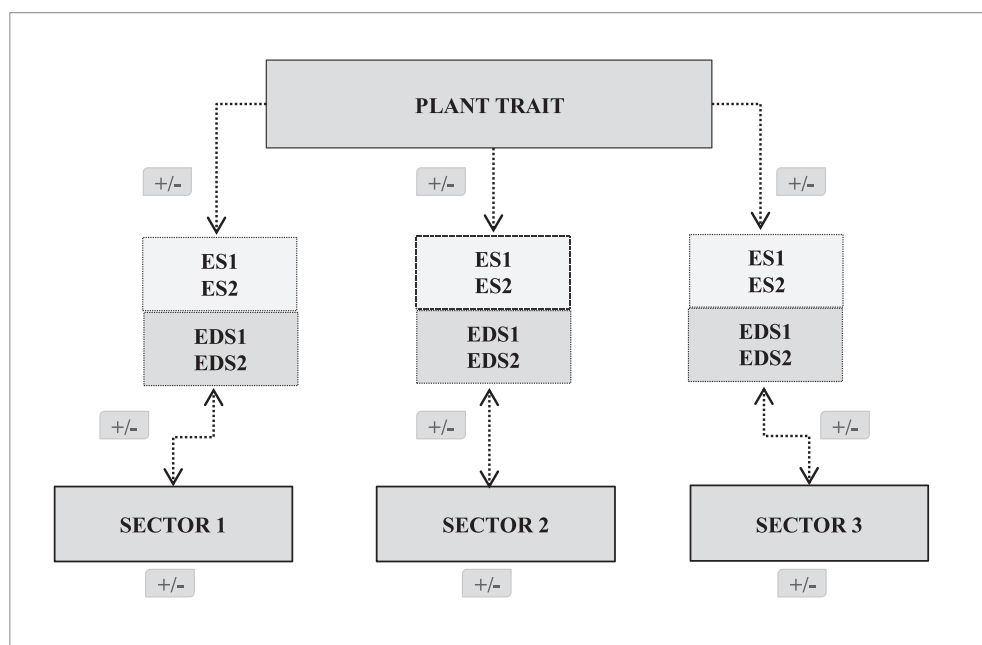


Fig. 2. Conceptual framework showing the linkage between a plant trait, ecosystem services, ecosystem disservices and different sectors (environmental/ socioeconomic) affected by IAS. Both, ES (light gray box - ES1, ES2) and EDS (dark gray box - EDS1, EDS2) can be increased (“+”) or decreased (“-”) by IAS, resulting in different types of benefits or impacts on sectors. Therefore, benefits are the result of a positive effect on ES or negative effect on EDS and impacts are an outcome of negative influence on ES or positive on EDS. Finally, if the strength of the influence is known (depending on the literature and data availability), it can be presented with the thickness of links between sectors and services (low impact – thin line, medium impact – thicker line, high impact – the thickest line). Moreover, the framework is applicable across all traits and plant species.

species via their traits to ES and EDS relevant in different socio-economic (agriculture, forestry, health) and environmental sectors (with ES such as carbon sequestration, erosion control, pollination). The main aim is to link *actors* (IAS and their traits) with *results/effects* (ES and EDS) they generate on different sectors by identifying the impacts and benefits. Thus, the framework comprises three parts: *plant trait*, *ecosystem services* and *disservices*, and *sectors*. It is intended to address the following questions: Which sectors (environmental/socio-economic) are most impacted by reduced ES/increased EDS contributed by invasive plants; what are the sectors benefiting from different increased ES/reduced EDS provided by invasive plants; which plant traits are predominantly responsible for influencing (positively or negatively via ES or EDS) different sectors; are there trade-offs in the effect caused by the same trait across sectors?

4.1. Plant traits

Plant traits were shown to be important for the provision of services and disservices. For example, canopy and root size affect various regulating services (climate and water regulation, soil stability) and the provision of food (de Bello et al., 2010). Leaf traits (leaf dry matter content, SLA and nitrogen content) affect soil fertility but also can be crucial for biocontrol and as a cultural service (ornamental value). For some legume species, traits such as corolla length are valuable for pollination efficiency (Lavorel et al., 2013). Phenological pattern in flowering (time and duration) is another characteristic affecting the provision of resources for pollinators (Lavorel et al., 2013). In woody plant species, tree height and biomass are principal traits impacting or enhancing provisioning services (timber and biofuel) and cultural services (aesthetic appreciation). Similarly, provisioning services (provision of food for humans or animals) are mainly affected by plant biomass (de Bello et al., 2010), either as the amount of food produced or as

decrease in crop yields (via competition or allelopathy). The example of biomass shows that effects of plant traits can be context dependent (can have a positive or negative effect on ES/EDS). However, species with similar life form or habitat might have similar effects on ES/EDS. Provided that the traits show a similar pattern between different IAS, the framework can be used as an efficient way of tackling their impact and can lead to faster interventions.

4.2. Sectors, ecosystem services and disservices

We assigned ES and EDS to six main public sectors influenced by invasive plant species: agriculture, forestry, infrastructure, human health, aesthetics and recreation, and environmental effect. Each of these sectors can have numerous services and/or disservices provided by IAS (Fig. 3).

IAS affect food production, timber, medicine, erosion control, via increasing or reducing these services. Moreover, invasive plants support or diminish disservices, such as pathogen transmission, and damage to infrastructure, human health or fire regimes. However, sometimes apparent disservices (e.g. allelopathy) can be perceived beneficial in specific circumstances or ecosystems (plants can produce and release allelopathic secondary metabolites affecting other plants and ecosystem, while the same chemicals can be used in pharmaceutical industry; Jimenez-Garcia et al., 2013). Identifying cumulative plants' effects (positive or negative) can simplify and improve decision making, particularly when multiple ES and EDS are considered.

5. Application of the framework

Traits of invasive plant species can affect an array of ES and EDS. Although these effects can be straightforward (e.g. increase in tree biomass provides more timber, pollen of a plant causes allergies etc.)

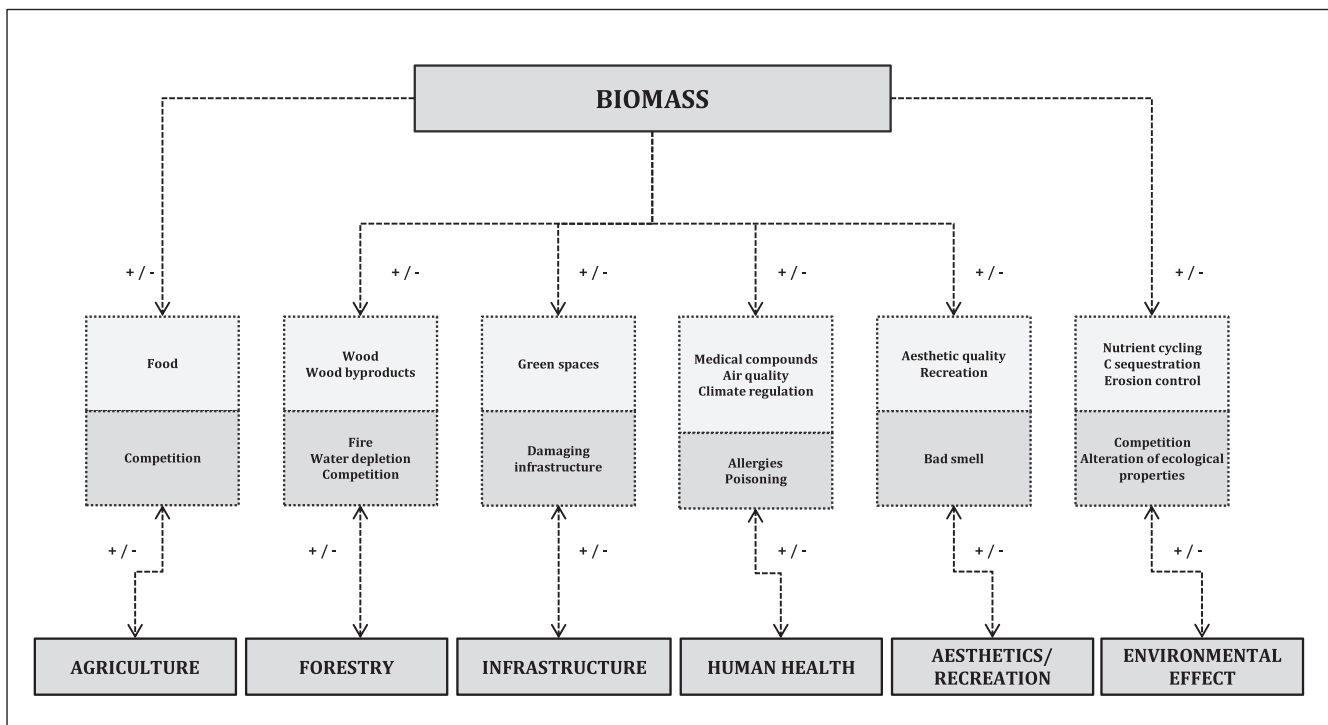


Fig. 3. Biomass (e.g. increase of biomass) as a trait of invasive species and its benefits (+) or impacts (-) on different sectors and ES (light gray boxes with dotted frame) and EDS (dark grey boxes with dotted frame).

often the effect is ambiguous or even antagonistic (simultaneous provision of both ES and EDS; Fig. 3). Below, we present several examples of plant traits with opposing effects (providing both, ES and EDS), where it can be beneficial to apply the framework for deciding on managing invasive species.

5.1. Tree canopy

Plant height and canopy height are traits that can have conflicting effects. For example, tree species can provide shade and climate regulation (ES), however, such shady places can be perceived as unsafe and as cover for burglars or wild animals (Lyytimäki and Sipilä, 2009; Potgieter et al., 2019).

5.2. Nitrogen-fixing plants

Black locust (*Robinia pseudoacacia*) is a nitrogen-fixing invasive plant species in Europe. It increases nitrogen in soil and litterfall, which can be a service in nutrient-poor tree plantations (Rice et al., 2004) or a reduced service where it negatively affects the diversity of non-nitrophilous species (Benespero et al., 2012).

5.3. Pollination type

Invasive plant species can be very attractive to pollinators and offer an additional food source. Brown et al. (2002) recorded a decrease in pollination of native *Lythrum alatum* in the presence of invasive *Lythrum salicaria*. Although food availability increased for pollinators (ES), visitation rates decreased for the native species, as well as pollen quality due to heterospecific transfer between the two species (EDS).

5.4. Toxicity

Leaves of nettle (*Urtica dioica*) are used as food and herbal medicine in many parts of the world. Yet, when uncooked its stinging leaves are painful in direct contact, and leaf's hairs can cause irritation or even be toxic for humans (Connor, 1977).

6. Use and data requirements

The conceptual framework has the advantage that it can be applied across multiple invasive species by using species traits as a fundamental unit. Simultaneously, the framework provides an overview of all (selected/observed/interesting/relevant) services and disservices (including whether they are positively or negatively affected, respectively) and highlights main sectors influenced by IAS. It hence brings into focus sectors that urgently need to be addressed and traits most relevant for positive or negative effects in several sectors (Box 1).

Box 1

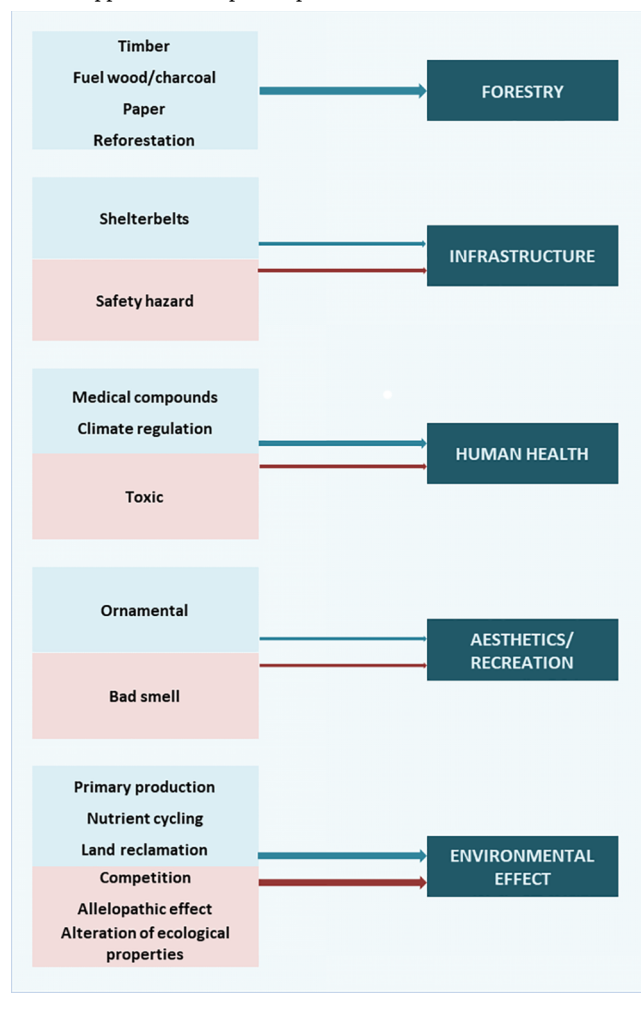
Framework application using invasive species *Ailanthus altissima* (from Sladonja et al., 2015).

Illustrative example of the stem height (biomass) effect as a functional trait of *A. altissima* (tree of heaven) on the (a) ES (left, blue boxes); (b) EDS (left, red boxes); (c) and different sectors (right, dark blue boxes). Benefits of *A. altissima* are presented using blue arrows, and impact via red arrows; the number of different services or disservices is illustrated with different arrow thickness (one ES/EDS – thin line, multiple ES/EDS – thicker line).

An increase in trunk biomass is a benefit for forestry, with the provision of wood and wood by-product and via reforestation. Overall, tree of heaven shows the biggest effect on ecological properties. Due to its very soft, light wood and great resistance property it is a good choice for planting to combat climate change (Enescu, 2014). Since it is often planted at former landfills or

mining areas it is useful for restoring derelict land. However, *A. altissima* is a very competitive species and produces allelopathic compounds in the bark. Finally, it affects N, organic C and pH in the soil (Kowarik and Sämel, 2007).

Plantations of *A. altissima* are used as a shelterbelt to control erosion or on sides of the highways, yet they can obstruct the view and therefore present safety hazard. Extracted components from tree of heaven are used in both traditional and conventional medicine. Nevertheless, the sap can be toxic to humans (Nentwig et al., 2017). Trees are suitable for growth in urban areas as they withstand high pollution levels and are valued for their ornamental appearance despite unpleasant odor.



The application of the conceptual framework requires data on species trait(s) and lists of ES and EDS provided with the effects quantified (or in some cases with qualitative data). Currently, studies quantify effects by (i) numerical scoring (e.g. 1 to 5 or 1 to 3), (ii) description (very high, high, moderate, low, none; Blackburn et al., 2014, Bacher et al., 2018, Nentwig et al., 2016, 2018), (iii) statistical significance (significant or non-significant impact; Pyšek et al., 2012b), (iv) monetization (costs or value; Cook et al., 2007), (v) percentage of increase/decrease (e.g. crop yields; Fried et al., 2017).

IAS have been classified with respect to their environmental impact – EICAT (Blackburn et al., 2014) and socioeconomic impact – SEICAT (Bacher et al., 2018) into several categories: massive, major, moderate, minor and minimal concern. This categorization was developed to help identify the magnitude of negative effects alien species have on the environment and human well-being. Similarly, classification can be established for benefits provided by IAS. Changes caused by IAS can be perceived as beneficial (increased ES/decreased EDS) or harmful

(increased EDS/decreased ES) by different people depending on their personal preference, financial status, cultural background or education (Shackleton et al., 2018, Potgieter et al., 2019). Therefore, the main advantage of our framework is that it is suitable for different types of data sets and that it allows flexibility in the choice of scoring systems. It can hence serve as a basis for further meta-analyses. Summarizing, our framework has several advantages: One can use multiple traits and/or multiple species when assessing the effects of IAS. Our framework addresses the “bigger picture” by assessing the effect of invasive species on sectors (and not only ES/EDS as in Vaz et al., 2017) and thus “opposing” effects (e.g. positive effect via one ES and impact via another reduced ES /EDS). In this case trait can have predominately negative effect in one sector (e.g. increases in biomass can impact wood production or biodiversity), and mostly positive in another (e.g. increases shade, regulates climate and has ornamental value). Therefore, these species can be considered undesirable in forest but beneficial in urban areas and parks. The framework allows assessing the interplay between different ES/EDS and is adjustable to any type of qualitative and quantitative data. Some traits link to multiple services (or disservices) but also there might be interactions among them including interactions between ES and/or EDS across sectors.

In addition to the framework’s advantages, some limitations exist. Due to lack of data, currently, the framework is predominantly applicable using qualitative data since quantitative data are infrequent in the literature. Similarly, it could prove to be difficult to assess if a certain effect is beneficial or disadvantageous. Thus, some traits can be considered ES or EDS depending on the context. Finally, in some cases, it can be challenging to link certain ES/EDS with the specific functional trait (and how much this trait exclusively contributes to ES/EDS). However, the framework can handle the dichotomy of ES and EDS, by allowing the integration of all diverging services and disservices and by focusing on the final outcome within sectors.

7. Conclusions

Invasive plant species provide some major services and disservices, directly affecting human well-being. Only recently part of the research agenda on biological invasions shifted toward examining both benefits by providing ecosystem services as well as disservices, e.g. as a direct negative effect of IAS on human well-being (Dobbs et al., 2014). We classified the main benefits and impacts IAS provide in Europe and disentangled the difference between services and disservices in the context of invasion biology. The conceptual framework uses traits of invasive plant species as a proxy for effects on different services and disservices. The framework provides a simple and comprehensive way of highlighting the main environmental and socioeconomic sectors affected by invasion while enabling the use of multiple (and often conflicting) services and disservices and thus linking plant traits with sectors. This is facilitated by applying the direction (positive/negative) and strength of impact. Clarifying the extent of impact and benefit as well as most affected sectors can help address problems caused by IAS.

Declaration of Competing Interest

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

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