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1 **Linking traits of invasive plants with ecosystem services and** 2 **disservices**

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18 **Highlights**

19 • Invasive alien species (IAS) can have negative as well as positive effects on human well-
20 being.

21 • The impact of IAS on ecosystems is mediated by species characteristics, some of which
22 relate to ecosystem service provision.

23 • The proposed framework examines the relationship between traits of invasive plants, and
24 ecosystem services and disservices.

25 • The framework supports the identification of plant traits which affect (positively and/or
26 negatively) different environmental and socioeconomic sectors of human well-being

27 **Abstract**

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

42 **Keywords**

43 Alien species, biological invasions, conceptual framework, ecosystem disservices, ecosystem
44 services, functional traits

45 **Introduction**

46 Alien plant species have been introduced by humans all over the globe and many of them have
47 become invasive (i.e. causing impact; see below). They have modified ecosystems for centuries
48 with great effects on the environment and human well-being (Vilà et al., 2010, Vilà and Hulme
49 2017). Alien species numbers have increased with the development of agriculture, forestry, and
50 industry (van Kleunen et al., 2015, Pyšek et al., 2017) and this increase is not yet saturated
51 (Seebens et al., 2017). Alien species were reported to have a great effect on agriculture, for
52 instance, in the US introduced species make up 98% of food consumed (Pimentel et al., 2005).
53 Similarly, plant species used in forestry or horticulture are often introduced, e.g. a study in the US
54 showed that 82% of tree species (out of 235) were introduced for landscaping, already in the 17th
55 century, when the first ornamental garden was founded (Reichard and White, 2001). At the same
56 time, there are hundreds of alien woody species (most commonly of the genera *Pinus*, *Eucalyptus*
57 and *Acacia*) commercially planted for timber (Holmes et al. 2009). Herbaceous plant species are
58 introduced as ornamentals in botanical gardens or private gardens because of their exotic
59 appearance (Hulme et al., 2018, van Kleunen et al., 2018) or for the production of pharmaceutical
60 and cosmetic compounds (Scott, 2010). In Europe, the majority of alien plant species were
61 introduced for agriculture, forestry, materials, horticulture or as ornamental species (Lambdon et
62 al., 2008). Further, alien species are used in ecosystem restoration, for soil stabilization, and as
63 phytoremediators or windbreakers (Pejchar and Mooney, 2009).

64 While ecosystem services (ES) present direct or indirect positive effects, disservices (EDS)
65 generate functions, processes and attributes in ecosystems that result in perceived or actual
66 negative impacts on human well-being (Shackleton et al., 2016). In this paper, we first introduce
67 invasive alien plant species and their environmental and socioeconomic effects. Further, we

68 present plant functional traits linked with invasiveness and ES / EDS. Additionally, we overviewed
69 main ES/EDS of invasive plant species in Europe as a rationale for a conceptual framework that
70 links IAS, traits and ES/EDS. Here, we used the Common International Classification of
71 Ecosystem Services (CICES; Haines-Young and Potschin, 2012) where ES can be classified as
72 follows: (i) provisioning services (including food, fiber, pharmaceuticals, water and others); (ii)
73 regulation and maintenance services (climate, water and erosion regulation, nutrient cycling,
74 pollination etc.); and (iii) cultural services (spiritual and aesthetic values as well as providing
75 foundation for tourism and recreation development).

76

77 **Background**

78 *Invasive plant species*

79 By now, 13,168 alien plant species have been reported as naturalized around the world (GloNAF
80 - Global Naturalized Alien Floras; van Kleunen et al., 2015, Pyšek et al., 2017, van Kleunen et al.,
81 2019), with highest numbers in North America (5958 taxa), Europe (4139) and Australasia (3886;
82 Pyšek et al., 2017). Most alien species that successfully naturalize in a new area (i.e. forming self-
83 sustaining populations by reproducing in the wild without human intervention and thus become
84 permanent parts of the flora; Richardson et al., 2000, Pyšek et al., 2012a), do not necessarily
85 modify their new habitat or cause positive or negative effect on environment or people. Vilà et al.
86 (2010) showed that 5–6 percent of alien plant species in Europe are noted to have an environmental
87 and socioeconomic effect. Estimates of the total numbers of invasive plant species over the globe
88 vary (e.g. 451 in Weber (2003), excluding agricultural weeds, or 672 in the CABI Invasive Species
89 Compendium; www.cabi.org/isc).

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

98

99 *Environmental and socioeconomic effects of IAS*

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

112 plants can have detrimental effects on ecosystems by altering nutrient and water cycles or
113 facilitating erosion (Kettunen et al., 2008).

114 Agriculture, forestry and tourism can profit from IAS, however economic costs of losses, damage
115 and control can exceed the profits they provide (Pimentel et al., 2005). For example, in the US,
116 IAS cause the major losses in crop production resulting in 26.4 billion dollar loss per year,
117 including a loss of 21 billion dollars by introduced pests and microbes (Pimentel et al., 2005).
118 Similarly, invasive pathogens result in considerable losses in forestry and recreation sectors – up
119 to 20.3 and 2 billion US dollars annually, respectively (Pimentel et al. 2005, Holmes et al., 2009).
120 Furthermore, there are additional economic and environmental costs resulting from eradication,
121 such as ecosystem recovery from the damages caused by herbicides or other weed removal
122 techniques (Pimentel et al., 2005). In the UK, Japanese knotweed (*Fallopia japonica*) causes
123 significant damages to infrastructure (roads, households, railways), with the costs of vegetation
124 management and eradication totaling 165 million pounds, annually (Williams et al., 2010). Finally,
125 IAS can decrease landscape quality and cause health problems (Kettunen et al., 2008, Pyšek and
126 Richardson, 2010, Sladonja et al., 2015, Lazzaro et al., 2018). Overall, in Europe, terrestrial
127 invasive plants cost 3.74 million euros annually, a third of total economic costs caused by all IAS
128 in Europe (Kettunen et al., 2008).

129 Nevertheless, some IAS can also have beneficial effects, manifested as increased provision of ES
130 or reduced EDS. They can, consequently, affect environmental and socioeconomic sectors
131 (agriculture, forestry, infrastructure, human health, aesthetics and recreation, environmental effect:
132 sectors adapted from categories by Kumschick et al., 2012) positively and negatively (Table 1).
133 For example, some plant invaders, such as *Ailanthus altissima*, can cause severe allergies in
134 humans, yet, the species is used in the pharmaceutical industry due to its beneficial chemical

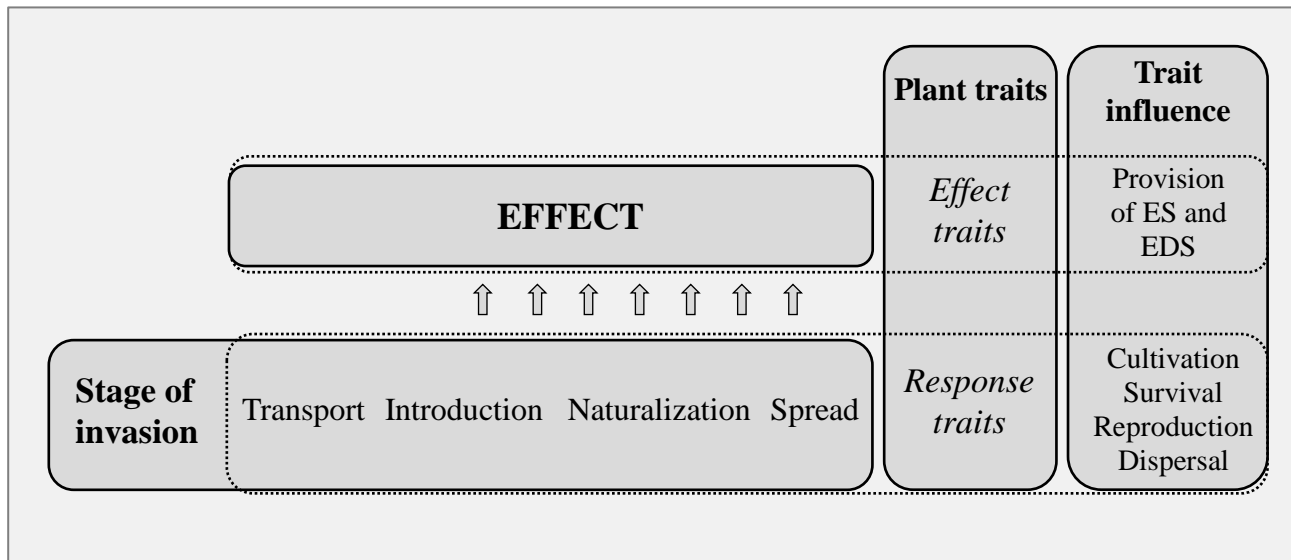
135 compounds (Sladonja et al., 2015). Ornamental species can increase the recreational value of the
136 landscape but also have an adverse effect on ecosystems by degrading habitats, reducing
137 biodiversity, causing injuries, and being toxic to humans (Potgieter et al., 2017). Invasive tree
138 species used for timber production can at the same time release chemical compounds via
139 allelopathy (Holmes et al., 2009) thereby inhibiting the growth of surrounding trees (decrease in
140 ES). Many ornamental broad-leaved trees emit biogenic volatile organic compounds, which
141 increase the concentration of ozone and photochemical smog in the atmosphere (Niinemets and
142 Peñuelas, 2008). The complexity of ecosystems and interactions between invasive and native
143 species makes identifying the real effects of invasive species difficult.

144

145 *Plant traits associated with invasiveness*

146 Many studies showed that certain functional traits of introduced plant species are associated with
147 their ability to become invasive (e.g. flowering period, clonality, height; Pyšek et al., 2015, Pyšek
148 et al., 2009, van Kleunen et al., 2010). In our paper, we consider functional traits as “any trait
149 which impacts fitness indirectly via its effects on growth, reproduction and survival” (Violle et al.,
150 2007). Some traits associated with plant invasiveness include: growth rate (IAS grow faster
151 compared with native species), SLA (higher specific leaf area in IAS), flowering phenology (IAS
152 start flowering earlier and have longer flowering periods), higher fecundity and more efficient seed
153 dispersal (Pyšek and Richardson 2007). Given the relationship of plant traits with plants’
154 invasiveness we argue that plant traits can be an important tool for predicting benefits (ES) or
155 impacts (EDS) for different environmental and socioeconomic sectors (Table 1): Traits do affect
156 ecosystem functions (Díaz et al. 2004), which humans might perceive as services or disservices

157 that can translate into societal (monetary or non-monetary) values (cf. ecosystem service cascade;
 158 Haines-Young and Potschin 2010).
 159 Thus, it is important to make a distinction (Fig. 1) between response and effect traits (Lavorel and
 160 Garnier 2002) in different stages of the invasion process, i.e. transport and introduction to a new
 161 area, establishment of self-sustaining populations (naturalization), and spread within the new area
 162 (Richardson et al., 2000).



163
 164 **Figure 1.** Different types of plant traits are important for each stage of invasion; response traits
 165 in early stages, while effect traits become more significant when introduced species begin to have
 166 an impact. However, the effect can be realized at any stage of the process.

167
 168 Response traits respond to environmental changes (e.g. life form, SLA, life cycle, relative growth
 169 rate, leaf and root morphology and seed mass; Lavorel and Garnier, 2002). Therefore, they are
 170 crucial throughout the invasion process, predominantly during the plants' establishment and spread
 171 phases when plants need to overcome environmental barriers (Richardson et al., 2000). Different
 172 traits may be beneficial in different phases of the invasion process (Richardson and Pyšek, 2012)

173 – such as ornamental traits that might decide which species are transported across countries at all
174 (Reichard and White, 2001). When IAS start to have an impact on ecosystems or economies, effect
175 traits become more relevant since they affect ecosystem functioning and the provision of ES or
176 EDS. These include, among others, plant height and biomass (competitive ability), phenology,
177 mutualism with nitrogen-fixing bacteria, longevity, leaf litter quality or photosynthesis pathway
178 (for example, in South Africa most of the invasive grass species are C3 and can have an advantage
179 over C4 species in disturbed ecosystems or with an increase of CO₂, e.g. more efficient nitrogen
180 use in grasses; Milton, 2004).

181 ***Plant traits and ES & EDS***

182 Plants' effects on ES (such as crop yields, cultural services, pollination) are manifested by
183 changing ecosystem functions and related values through the agency of functional traits such as
184 biomass, plant height, canopy and root size/architecture, leaf dry matter content, SLA, soil organic
185 carbon, flowering pattern or leaf P/N concentration (de Bello et al., 2010, Lavorel et al., 2011).
186 Based on the frequency of certain traits, ecosystems may become “hot-spots” of ecosystem
187 services, fostering multiple services provided by some species (Potgieter et al., 2017), or they can
188 exhibit trade-offs between services and disservices as a result of contrasting traits. Some tree
189 species, due to their fast growth contribute carbon sequestration, climate regulation or erosion
190 control (ES), while this trait can lead to increase in fire risk (EDS; Castro-Díez et al., 2019). For
191 example, Millward and Sabir (2011) showed that the effect of maple (*Acer platanoides*) on air
192 quality is two-fold; it sequesters carbon dioxide from the air while emitting biogenic volatile
193 organic compounds, which significantly reduce air quality. Such trade-offs can be expressed as a
194 conflict between service and disservice.

195 In summary, the extent and direction of IAS' effects on ES and EDS can be ambiguous. Thus, it
196 is necessary to create a framework that provides information on which plant species should be
197 prioritized for management actions in which environmental or socioeconomic sectors, depending
198 on their traits and thus their positive and negative effects. Our paper provides a framework which
199 is an extension of existing frameworks (e.g. Vaz et al., 2017). It examines the relationship of
200 (functional) traits of invasive plants with ecosystem services and disservices, by linking those traits
201 to affected sectors (agriculture, forestry, infrastructure, human health, aesthetics and recreation,
202 and environmental effect).

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

207

208 **Main ES and EDS provided by invasive plant species in Europe**

209 In order to identify the benefits (increase in ES/ decrease in EDS) and impacts (increase in EDS/
210 decrease in ES) of invasive plant species (Table 1), we chose 18 vascular plant species from the
211 list of representative invasive species in Europe provided by DAISIE (2009) and surveyed the
212 literature for information on how these species affect ES/EDS. The main aim was to get an
213 overview of ES and EDS provided by the selected invasive plant species in Europe. The main
214 criterion for a species to be included on the DAISIE list was, besides it being classified as invasive
215 in Europe, to cover a range of representative taxa and their impacts (Pyšek and Richardson, 2012),
216 which makes the selection suitable for the purpose of our study. We listed the ES and EDS

217 mentioned in the investigated literature with the direction of their effects (positive or negative;
218 Table 1). For example, for *Fallopia japonica*, the ES reported are the provision of animal food,
219 use in medicine, use as a pesticide and biofuel, and ornamental value (Table 1). However, *F.*
220 *japonica* negatively affects infrastructure, can cause floods (thick plant shoots can block water
221 flow; Palmer 1990, Colleran and Goodall, 2014), produces allelopathic chemicals and changes of
222 habitat (Murrell et al. 2011).

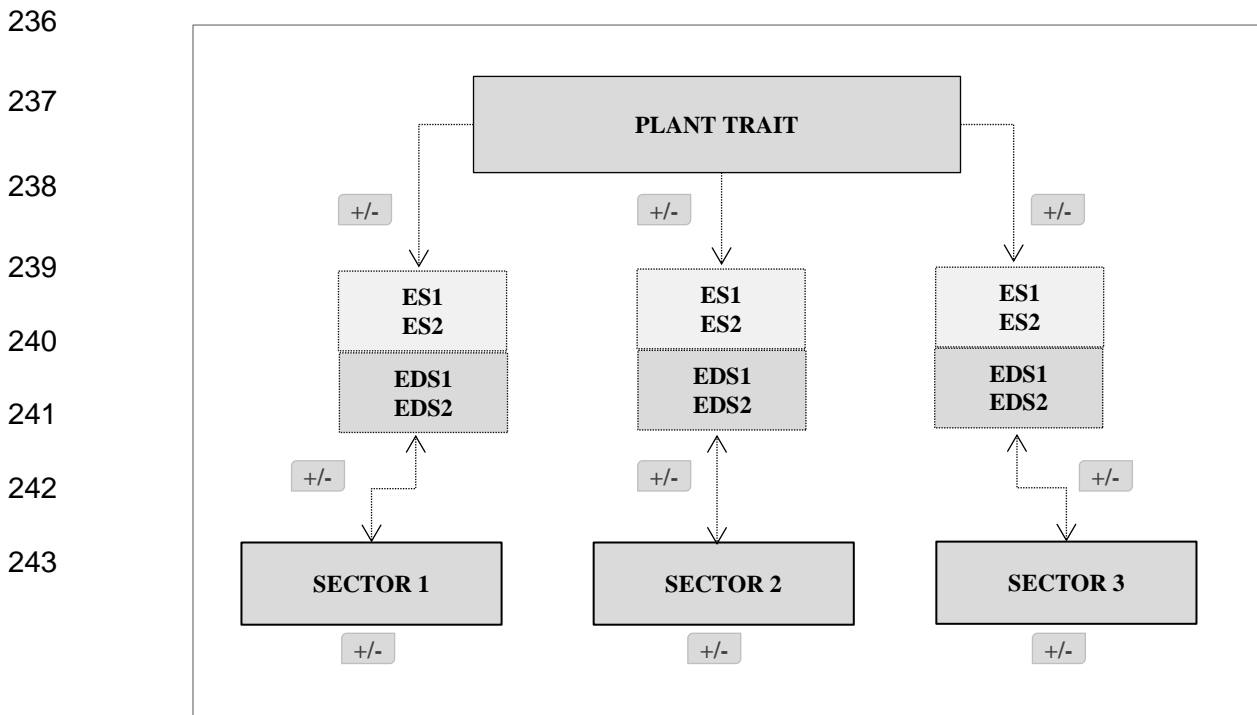
Table 1. List of effects on ecosystem services (increase and reduction in ES) and disservices (increase and reduction in EDS) provided by invasive plant species in Europe - (+): Increase in ES or EDS; (-): Decrease in ES or EDS

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-Diez 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>	Ornamental (+) ; Biodiversity (-);	Habitat alteration (+);	Biermann & Daniels, 1997; Daniëls et al. 2008;
<i>Carpobrotus edulis</i>	Ornamental (+) ; Soil stabilization (+) ; Use in traditional medicine (+) ; Used as food (+); Biodiversity (-);	Habitat alteration (+);	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 (+);	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 (-);	Erosion (+);	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 & Kollmann, 2009; Weidema, 2006; Dobson et al. 1990; Dubey et al. 2010; Bruun, 2006;

224 Conceptual Framework

225 We propose a novel framework (Fig. 2) linking invasive plant species via their traits to ES and
226 EDS relevant in different socioeconomic (agriculture, forestry, health) and environmental sector
227 (with ES such as carbon sequestration, erosion control, pollination). The main aim is to link *actors*
228 (IAS and their traits) with *results/effects* (ES and EDS) they generate on different sectors by
229 identifying the impacts and benefits. Thus, the framework comprises three parts: *plant trait*,
230 *ecosystem services* and *disservices*, and *sectors*. It is intended to address the following questions:
231 Which sectors (environmental/socioeconomic) are most impacted by reduced ES/increased EDS
232 contributed by invasive plants; what are the sectors benefiting from different increased ES/reduced
233 EDS provided by invasive plants; which plant traits are predominantly responsible for influencing
234 (positively or negatively via ES or EDS) different sectors; are there trade-offs in the effect caused
235 by the same trait across sectors?



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

254 **Plant traits**

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

267 context dependent (can have a positive or negative effect on ES/EDS). However, species with
268 similar life form or habitat might have similar effects on ES/EDS. Provided that the traits show a
269 similar pattern between different IAS, the framework can be used as an efficient way of tackling
270 their impact and can lead to faster interventions.

271 *Sectors, ecosystem services and disservices*

272 We assigned ES and EDS to six main public sectors influenced by invasive plant species:
273 agriculture, forestry, infrastructure, human health, aesthetics and recreation, and environmental
274 effect. Each of these sectors can have numerous services and/or disservices provided by IAS (Fig.
275 3).

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

284 **Application of the framework**

285 Traits of invasive plant species can affect an array of ES and EDS. Although these effects can be
286 straightforward (e.g. increase in tree biomass provides more timber, pollen of a plant causes
287 allergies etc.) often the effect is ambiguous or even antagonistic (simultaneous provision of both
288 ES and EDS; Fig. 3). Below, we present several examples of plant traits with opposing effects
289 (providing both, ES and EDS), where it can be beneficial to apply the framework for deciding on
290 managing invasive species.

291 ***Tree canopy***

292 Plant height and canopy height are traits that can have conflicting effects. For example, tree species
293 can provide shade and climate regulation (ES), however, such shady places can be perceived as
294 unsafe and as cover for burglars or wild animals (Lyytimäki and Sipilä, 2009; Potgieter et al.,
295 2019).

296 ***Nitrogen-fixing plants***

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

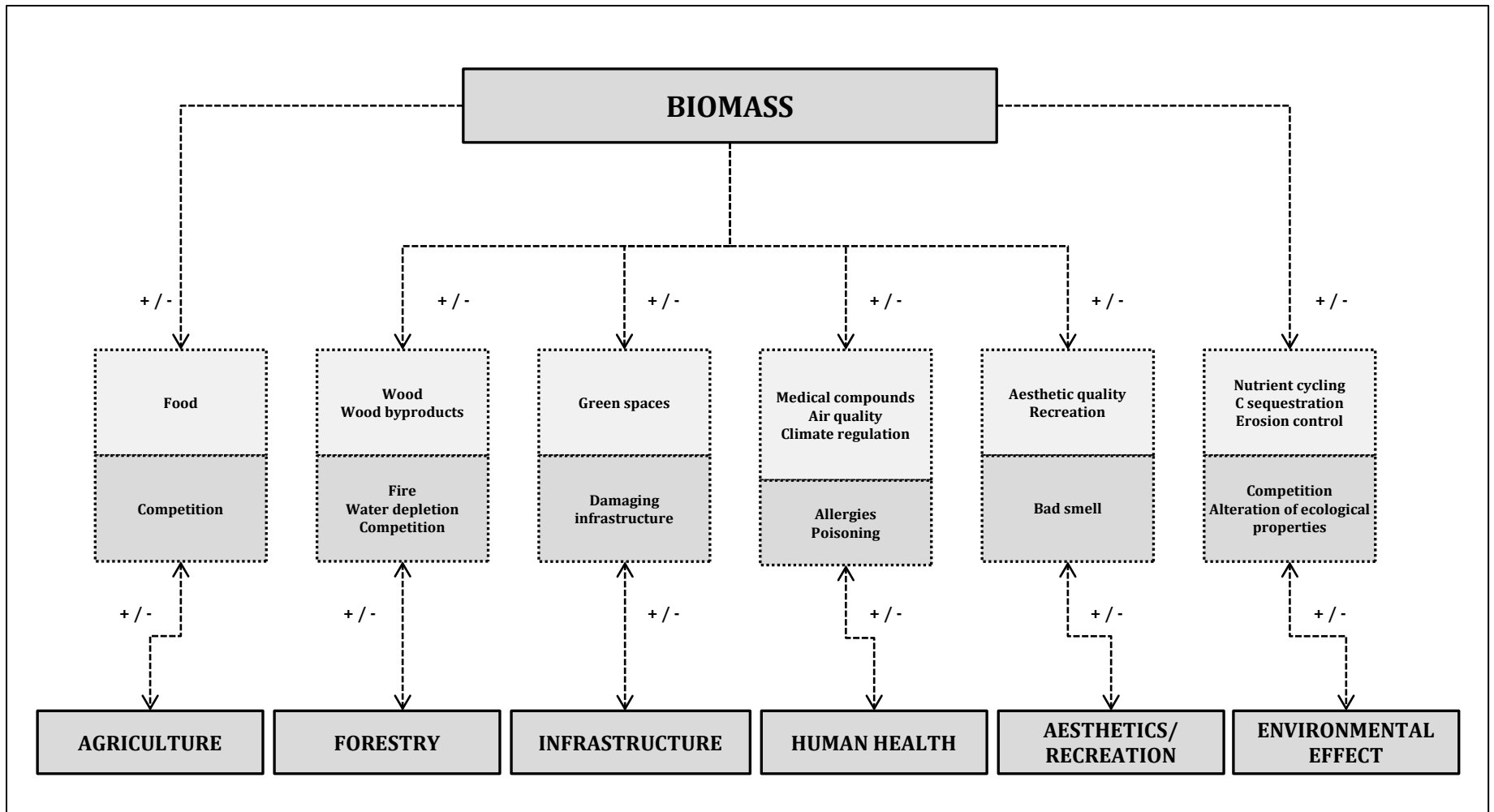
301 ***Pollination type***

302 Invasive plant species can be very attractive to pollinators and offer an additional food source.
303 Brown et al. (2002) recorded a decrease in pollination of native *Lythrum alatum* in the presence of
304 invasive *Lythrum salicaria*. Although food availability increased for pollinators (ES), visitation

305 rates decreased for the native species, as well as pollen quality due to heterospecific transfer
306 between the two species (EDS).

307 ***Toxicity***

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



311

312 **Figure 3.** Biomass (e. g. increase of biomass) as a trait of invasive species and its benefits (+) or impacts (-) on different sectors and

313 ES (light gray boxes with dotted frame) and EDS (dark gray boxes with dotted frame)

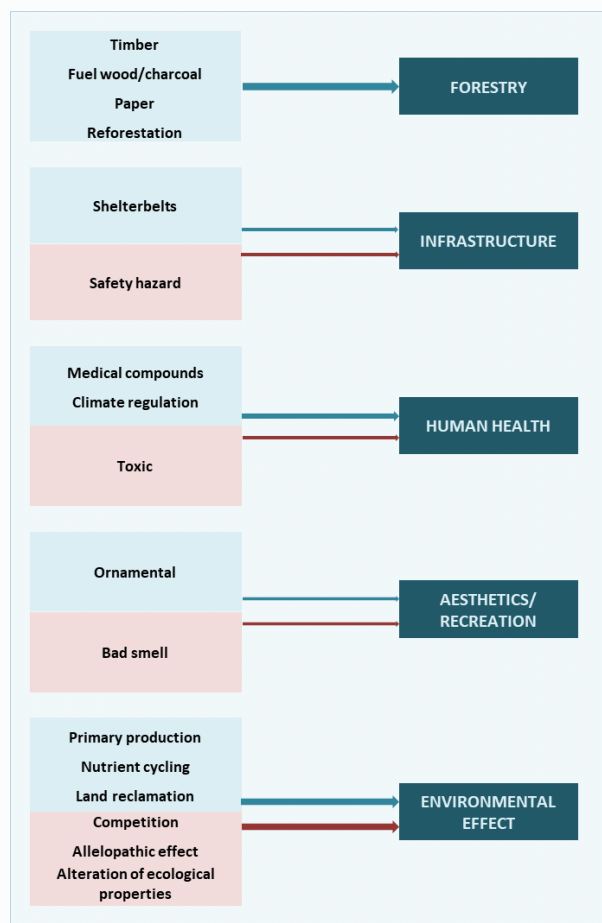
314 Use and data requirements

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



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

328 IAS have been classified with respect to their environmental impact – EICAT (Blackburn et al.,
329 2014) and socioeconomic impact – SEICAT (Bacher et al., 2018) into several categories: massive,
330 major, moderate, minor and minimal concern. This categorization was developed to help identify
331 the magnitude of negative effects alien species have on the environment and human well-being.
332 Similarly, classification can be established for benefits provided by IAS. Changes caused by IAS
333 can be perceived as beneficial (increased ES/decreased EDS) or harmful (increased EDS/decreased
334 ES) by different people depending on their personal preference, financial status, cultural
335 background or education (Shackleton et al., 2018, Potgieter et al., 2019). Therefore, the main
336 advantage of our framework is that it is suitable for different types of data sets and that it allows
337 flexibility in the choice of scoring systems. It can hence serve as a basis for further meta-analyses.
338 Summarizing, our framework has several advantages: One can use multiple traits and/or multiple
339 species when assessing the effects of IAS. Our framework addresses the “bigger picture” by
340 assessing the effect of invasive species on sectors (and not only ES/EDS as in Vaz et al., 2017)
341 and thus “opposing” effects (e.g. positive effect via one ES and impact via another reduced ES
342 /EDS). In this case trait can have predominately negative effect in one sector (e.g. increases in
343 biomass can impact wood production or biodiversity), and mostly positive in another (e.g.

344 increases shade, regulates climate and has ornamental value). Therefore, these species can be
345 considered undesirable in forest but beneficial in urban areas and parks. The framework allows
346 assessing the interplay between different ES/EDS and is adjustable to any type of qualitative and
347 quantitative data. Some traits have multiple services (or disservices) but also there might be
348 interactions among them including the ES/EDS interaction between different sectors.

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

357 **Conclusions**

358 Invasive plant species provide some major services and disservices, directly affecting human well-
359 being. Only recently part of the research agenda on biological invasions shifted toward examining
360 both benefits by providing ecosystem services as well as disservices, e.g. as a direct negative effect
361 of IAS on human well-being (Dobbs et al., 2014). We classified the main benefits and impacts IAS
362 provide in Europe and disentangled the difference between services and disservices in the context
363 of invasion biology. The conceptual framework uses traits of invasive plant species as a proxy for
364 effects on different services and disservices. The framework provides a simple and comprehensive
365 way of highlighting the main environmental and socioeconomic sectors affected by invasion while

366 enabling the use of multiple (and often conflicting) services and disservices and thus linking plant
367 traits with sectors. This is facilitated by applying the direction (positive/negative) and strength of
368 impact. Clarifying the extent of impact and benefit as well as most affected sectors can help address
369 problems caused by IAS.

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551 **Appendix 1: References from the species classification table (Tab. 1a, b)**

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