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# Invasive woody plants in the tropics: a delicate balance between control and harnessing potential benefits. A review

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## Abstract

The occurrence and spread of invasive woody species are a truly global phenomenon, but tropical regions seem to be particularly vulnerable due to high rates of soil degradation in combination with climate change, and limited resources for containment. There is increasing awareness that complete eradication programs are often not effective. The existence of many “controversial species,” i.e., species with both negative and positive impacts, renders decision-making processes for management exceedingly complex. By providing a very extensive overview of the current state of knowledge on impacts and containment strategies of invasive woody species, we aim to help underpin such decisions. We discuss both negative impacts and potential benefits of invasive woody species, focusing on the two most important ones, namely animal fodder production and the positive impacts on soil functioning and soil quality. Invasive woody species can positively impact livestock production (1) indirectly by improving pasture quality because of improved soil quality and functioning, and (2) directly by supplying a high-quality protein component for animal fodder. Invasive woody species increase soil carbon sequestration and nitrogen and phosphorus availability depending on the density of the invader, its capacity to fix nitrogen, the quantity and quality of its litter, and the direct interactions between its roots and the soil microbial community. The balance between potential benefits and risks depends to a large extent on the interaction with the local environment (climate, soil, vegetation, and animals) and the socioeconomic context of each region. When an invasion process starts because there is no local predator, then management can target eradication or very strict containment. If the invasion is the result of strong disturbance of the ecosystem, then intensive but well-thought management of the invasive species would be the choice to be made, as this may help to restore the ecosystem.

**Keywords** Invasive woody plants · Soil impact · Management strategies · Potential benefits

## 1 Introduction

The arrival and settlement of exotic plants in the Earth's ecosystems are to some extent a natural phenomenon and as old as the migratory processes of humans and animals (Binggeli 2001; Horvitz et al. 2017). Although the onset of the (un)intentional spread of exotic plants by human intervention cannot be accurately established, the Sumerians may have been the first civilization to engage in international trade in aromatic spices via the Arabian Peninsula and Mediterranean Sea as early as from 3000 BC (Guix et al. 2001; López and Page 2018). Many woody species have been introduced and spread into new regions because of the expansion of global trade, military expeditions, agriculture, and many other human activities (Dehnen-Schmutz et al. 2007; Aguin 2012). The discovery of the New World

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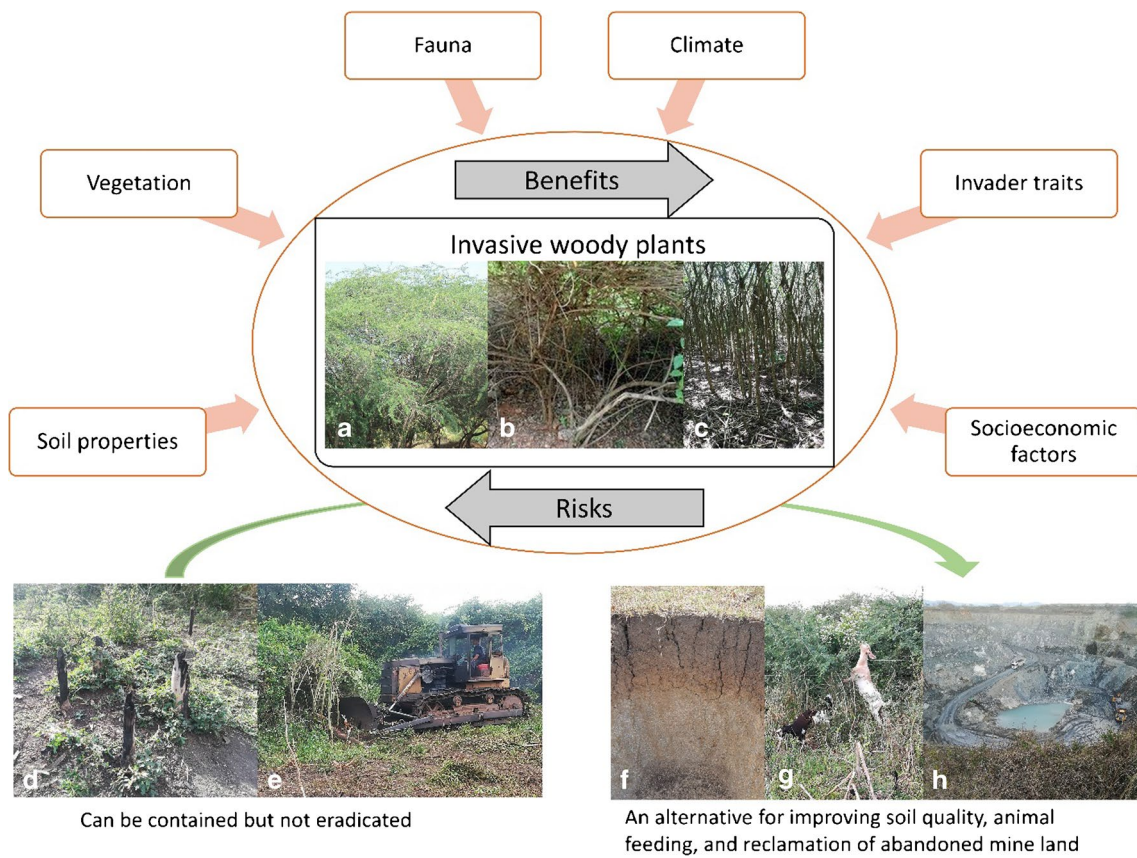
marked the beginning of the introduction of many woody plant species from Europe to the Americas and vice versa (e.g., introduction of *Robinia pseudoacacia* to Europe from the Americas during the sixteenth century [Guix et al. 2001] and *Cytisus scoparius* introduced in North America from Europe after 1800 [Reichard and White 2001]). During the period of European exploration and colonization, the exchange of exotic species was greatly accelerated by the creation of botanical gardens spread throughout the tropics during the seventeenth till nineteenth centuries (e.g., botanical gardens of Mauritius, Réunion, and Java in the Indian Ocean Saint-Domingue, Martinique, Guadeloupe, Guiana, Cayenne, and St. Vincent in the Caribbean [McCook 2011] Sydney Gardens in Australia, Rio de Janeiro Botanical Garden in South America, and Cape Town Botanic Garden in Africa [van Kleunen et al. 2018]).

Although the issue of invasions of exotic woody plants was and continues to be a global phenomenon with proven adverse effects on the biodiversity of impacted ecosystems, only in recent years there has been an increase in research addressing this issue with a focus more oriented to the socio-economic and environmental benefits that these species may offer. For many specialists, the current debate is centered on the question: “eradication or management through utilization?” In this sense, in the SCOPUS research database alone, we have identified at least 180 papers that discuss the conflict between forms of invasion management based either on negative impacts versus potential benefits, with 60% of these papers published in the last 10 years. Three of the reasons for the growing interest are (i) the high prevalence of invasive woody plants in many tropical grassland, savanna, and dry forest ecosystems in South America, Africa, Asia, and parts of Australia, due to high and still increasing degrees of forest fragmentation and soil degradation (Liao et al. 2006; Richardson and Rejmanek 2011; Wilcox et al. 2018), (ii) the incipient knowledge of which species have invaded, as well as the ecological consequences of this threat within the region compared to what is known in other regions (Herrera et al. 2017), and (iii) fragility of tropical soils compared to those of temperate climates, which makes them particularly sensitive to plant invasions (Juo and Franzluebbers 2003; Lal 2019). Three of the most significant drivers of the increase of invasive woody populations in tropical regions are presence of ecosystem disturbances (e.g., fire suppression, increased availability of resources such as nutrients and/or light by anthropogenic pressures, absence or decrease of natural enemies that regulate populations, habitat fragmentation, deforestation), the limited financial and infrastructural resources for the prevention or control of invasive plants (Tye 2009; Keppel et al. 2014), and climate change (e.g., increasing atmospheric carbon dioxide concentrations [Bond et al. 2003], hurricane passage [Bellingham et al. 2005], and changing temperature and precipitation patterns [Stevens

et al. 2017]). Increased climate change-induced woody plant invasions have been observed in Borneo (Osunkoya et al. 2005), Ethiopia (Shiferaw et al. 2019), Australia (Hardesty et al. 2011), India (Mungi et al. 2018), Japan (Yamashita et al. 2000), and Jamaica (Bellingham et al. 2005), to name just a few countries and cases.

Assessing the impacts of these plants on tropical ecosystems is becoming a controversial issue that requires context-specific assessment (Fridley et al. 2007). The reasons for so much controversy center on the fact that the potential losses that can be derived from invasions, as well as the benefits, are likely to be not a static issue, but rather something dynamic that depends on the species itself, the receiving ecosystem, and the human factor, i.e., the values that are incorporated in impact assessments and that may be different between and within societies (Bartz and Kowarik 2019). For example, the existence of “controversial species,” i.e., species with both negative and positive impacts, makes decision-making regarding the management of these species highly complex (Badalamenti et al. 2020). This is the case of species such as *Dichrostachys cinerea*, *Acacia* spp., *Prosopis juliflora*, *Leucaena leucocephala*, and *Cedrela odorata* which are considered to have a high invasive potential, yet promote various ecosystem services (e.g., provision of shade, forage for animal feed, stock-proof living fences, promote nitrogen fixation, carbon sequestration, erosion control, and can be used for ornamental, medicinal, etc. purposes, Richardson et al. 2004; De Angelis et al. 2021; Van der Meersch et al. 2021). On the other hand, efforts to completely eradicate these species have been unsuccessful in most—if not all—cases, due to the high costs of clearing or the persistence of seed banks in the soil (Fig. 1). Several studies demonstrate this reality with species such as *Rubus niveus* on Santiago Island, Galapagos archipelago (Renteria et al. 2012), *Lantana camara* in Hawai’i (Meyer 2014), *Prosopis* spp. in India (Bartlett et al. 2018), and *Dichrostachys cinerea* in Cuba (Pérez et al. 2015) which has reoriented the management of these species towards more ecosystem-friendly approaches and with attention to the potential benefits for the local population.

Regarding the specific impact of invasive woody plants on the soil, there is also much debate. So far, studies on this topic reflect a wide range of views regarding the role of these species in soil biogeochemical processes, i.e., the water cycle, litter decomposition rates, microbial functioning, and nutrient cycling (Leicht et al. 2015; Ruwanda and Shackleton 2016; Acharya et al. 2018). Several studies have documented the role of woody invaders in improving soil properties and fertility in a general sense, e.g., *Prosopis juliflora* (El-Keblawy and Al-Rawai 2007), *Mikania micrantha* (Chen et al. 2009), *Lantana camara* (Ruwanda and Shackleton 2016), *Acacia salicina*, *Pinus halepensis*, and *Eucalyptus occidentalis* (Jeddi et al. 2009), but these improvements



**Fig. 1** Invasive woody plants (a–c), management (d–e), and their potential contribution to, e.g., improving soil quality (f), livestock production (g), and restoring heavily disturbed ecosystems such as mining sites (h). Left, invaded areas by *Prosopis juliflora* (a - image Wikimedia commons), *Lantana camara* (b - image Wikimedia com-

mons), and *Dichrostachys cinerea* (c - image Z. González). Right, soil profile (high in soil organic matter and good structure) following 25 years of *Dichrostachys cinerea* invasion, goats feeding on invasive shrub, and abandoned mine (f–h image Z. González).

are very soil specific and depend on agroforestry practices. In this respect, the role of biological N fixation of many introduced agroforestry species is particularly important, and various studies have documented significant increases in N stocks when agroforestry practices are implemented with N-fixing species (Sileshi et al. 2014), many of which though are considered invasive. Such results contradict the narrow-minded historical view that monocultures are the best option for productivity in agriculture, horticulture, and forestry, and that have long prevailed. A review of Sileshi et al. (2014) showed that the annual N inputs vary widely between N-fixing invasive woody species and even within the same species across different locations and stand age.

The fact that research has come to ambiguous or contradicting conclusions as demonstrated above is one of the reasons for frequent controversies and conflicts of interest surrounding the management of invasive species (Crowley et al. 2017). For example, in a meta-analysis, Zhang et al. (2019) found that leaf litter and rhizosphere of woody invaders differentially affected soil bacterial biomass, leading to

increases and decreases, respectively. The invasion of coexisting species can also provoke differential impacts (e.g., stronger effects or neutralization of effects). In this sense, Mahla and Mlambo (2019) demonstrated that the effects of co-invasion of *Lantana camara* and *Dichrostachys cinerea* had neutral impacts on soil pH and soil moisture compared to the impacts of single species, while soil C and N in co-invaded plots were higher than in plots invaded by a single species.

Considering (a) soil as the key intermediary for all processes occurring upon introduction of invasive species, (b) its rapid degradation in many tropical areas (Nyssen et al. 2009; Lal 2019), (c) the progression of naturalized species becoming invasive, and (d) the impossibility of completely eradicating these invasive species, the potential role of invasive species in preserving or even improving soil quality urgently needs more attention. Therefore, this review has a strong focus on soil-related aspects of invasive woody species, and it also attempts to compile local, national, and regional experiences on management of woody plant invasions in the tropics (strongly

impacted by climate change) in view of the impact on soil quality. While in the past 30 years there has been a global initiative to promote much greater use of indigenous woody species in farming systems (Leakey et al. 2012), with an amazing uptake in the last decade (e.g., Leakey et al. 2022), here we will only focus on exotic invasive woody species, given the specific challenges they present.

To gain a better understanding of the impact of invasive woody plants in the tropic and its connectivity with management strategies for control or for harnessing possible benefits in the agricultural sector, (1) we critically discuss how “invasive woody plants in the tropics” have so far been defined in the literature, showing the fuzzy areas and contradictions of this concept, (2) we compile knowledge on the current extent of woody plant invasions in tropical regions and its evolution, (3) we discuss the options of eradication versus containment as a function of the invaded ecosystem properties, and (4) the potential benefits of invasive woody plants for agriculture, focusing on the crucial aspects of soil quality and provision of animal fodders, and finally (5) we analyzed the role of management strategies for invasion control and their impact on general soil quality.

## 2 Methods

A broad literature search was conducted in the electronic databases of Web of Science, Scopus, Elsevier, and Google Scholar using following broad search terms: (“invasive woody plants”), (“shrub encroachment”), (“woody plant invaders”). Further refining was also done using combinations of the above terms with “eradication,” “N-fixing” or “N-fixation,” “integrated management,” and “water cycle.” We did not specify the regions of interest (tropics) in this search, but rather removed articles with case studies from temperate and cold zones manually, in order to minimize the chance of un-deliberately excluding case studies on the tropics. This search resulted in the selection of a total of 278 relevant peer-reviewed publications in the abovementioned electronic databases which formed the basis for this review. Furthermore, we also checked the references cited within these primary sources and included relevant papers identified in that way also in the review. The literature search was terminated in May 2022, but additional literature was collected in the way depicted here in the period December 2022–January 2023, on the revision process.

## 3 Understanding the difference between “naturalized” and “invasive” woody plants

The concepts associated with the terms “invasion” and “naturalization” are often confused especially if no reference is made to environmental or economic impact. According to

Richardson et al. (2000), one problem involves the widespread use of naturalized species as a synonym for “invasive species,” thus lumping two overlapping, but not identical, phases in the naturalization/invasion process. The process of naturalization of a species begins with the intentional or unintentional introduction of the plant (or its propagule) to a new habitat (exotic plant). If during this period the species can overcome local abiotic and biotic barriers to develop self-sustaining populations, undergoes widespread dispersal, and becomes incorporated within the resident flora for at least 10 years without direct human intervention, then it is considered a naturalized species (Richardson et al. 2000; Kairo et al. 2003). Some researchers argue that only a very small number of introduced species naturalize (Denslow and Guzman 2002; Widrlechner et al. 2004). Naturalized plants thus self-multiply, distinguishing them from casual plants (i.e., plants that do not persist for more than one life cycle and thus need repeated introductions, Richardson et al. 2004) and can in this way expand, potentially becoming invasive species (Fig. 2). Some studies have highlighted the plant characteristics, or the mechanisms used by naturalized woody plants to successfully establish and spread (Table 1).

Invasive woody species are therefore a subset of naturalized plants that generally have a superior ability to occupy and maintain space, as well as the potential for rapid growth, particularly in non-resource-limited environments, establishing self-regenerating populations and have spread beyond their area of introduction (Richardson et al. 2000; Kairo et al. 2003; Leishman et al. 2007; Fleming et al. 2017; Shiferaw et al. 2019). Many of these invasive species can spread by vegetative propagation, an aspect that (a) secures colonization of unoccupied ground, (b) increases competitive power of the species within the community, and (c) increases survival rate in marginal habitats (Jeník 1994). While some of these characteristics or mechanisms are not exclusive of invasive plants, they play an important role in the impact of the invasive species.

The concept of “invasive plant” is complex and evolving, and research to date has followed two lines of thought regarding causes of invasion: (1) the process of invasion is one of the symptoms of a degraded ecosystem, and in that sense the invasive species could be considered a “pioneer plant” for the ecosystem that has evolved under environmental pressures to become a “new” ecosystem. For example, *Lantana camara* can withstand environmental stresses in new environments due to selection pressure and respond quickly to anthropogenic disturbances (Sakai et al. 2001; Negi et al. 2019); (2) the invasion can occur in undisturbed ecosystems (Gurvich et al. 2005; Martin et al. 2009) due to a lack of local predators. One well-documented example is the invasive Australian tree fern *Cyathea cooperi* that in the absence of the pathogens of their native habitat has been shown to be extremely efficient at utilizing soil nitrogen and

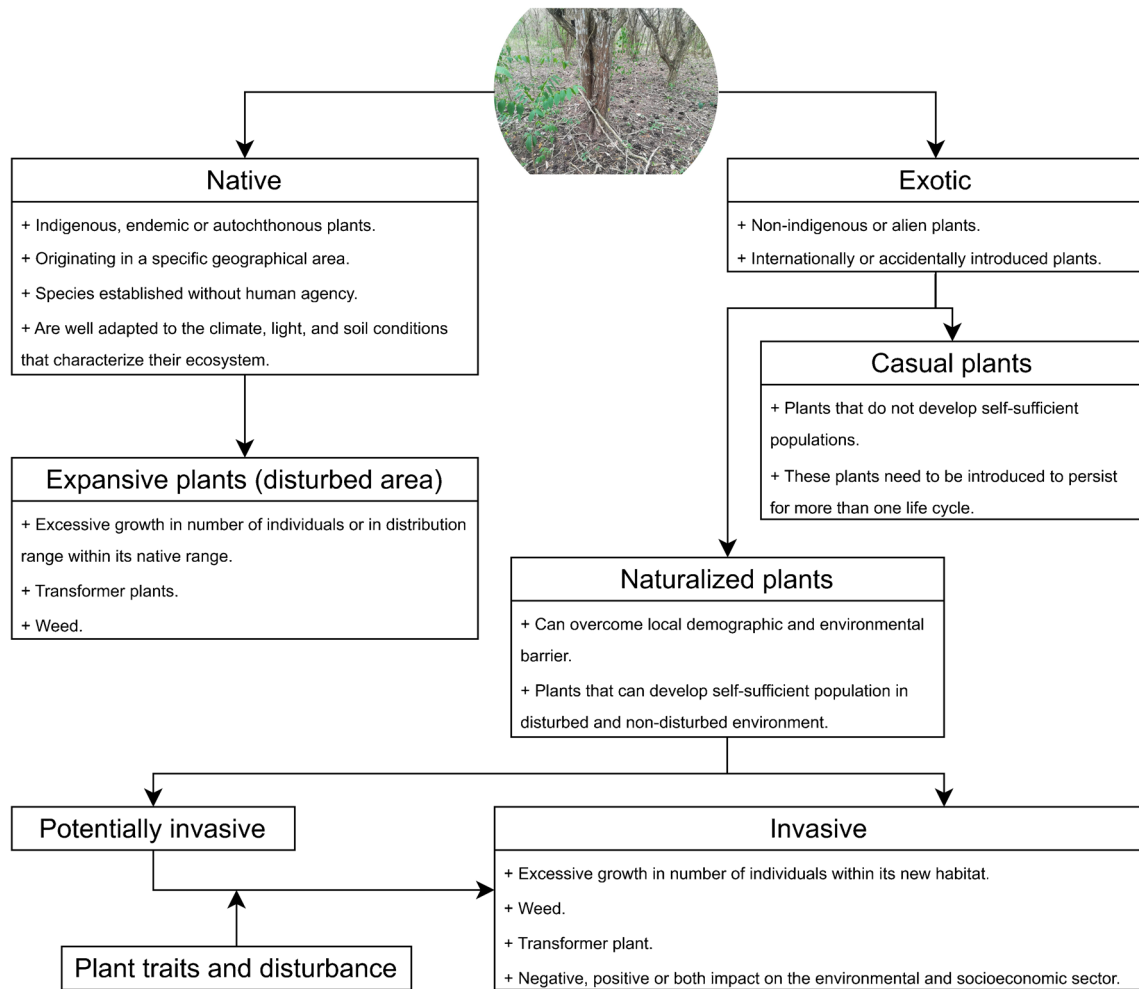


Fig. 2 Conceptual diagram of the origin of invasive woody plants.

to grow six times more rapidly in height than the native Hawaiian endemic tree ferns, *Cibotium* spp. (Durand and Goldstein 2001a, 2001b). Other similar examples are *Psidium guajava* in western Uganda (Sheil et al. 2000) and *Climexia hirta* in Malaysia (Peters 2001).

Although some species are well defined in terms of the type of ecosystem they invade, other species can colonize both disturbed and undisturbed environments, as is the case of two invasive woody species, *Ligustrum lucidum* and *Pyracantha angustifolia* in Argentina. While these species can expand faster in disturbed areas, they also invade areas with no or little disturbance (Gurvich et al. 2005).

From the above, it is essential to realize that attributes such as “naturalized” and “invasive” cannot refer to species in isolation but should necessarily be used in a specific ecosystem context. In addition, the invasive species may have both damaging and beneficial effects on the ecosystems that they invade. In the tropics, damaging effects may be a (further) decrease of biodiversity, disruption of the water

balance, collapse of farm yields, whereas beneficial effects include protection of the soil against erosion, increase of soil nutrient content, C sequestration, production of fodders, production of wood, among others. Therefore, rather than focusing on invasive species or the invasion process as such, this review analyzes the many interactions between invasive species and invaded ecosystem, with a strong emphasis on the soil-related processes, for the reasons outlined in the Introduction section.

#### 4 Current extent of invasive woody plants in the tropics

It is a fact that the phenomenon of woody plant invasions is global in nature. We have plotted the evolution of the number of invasive woody species in the tropics and subtropics between 1996 and 2014 based on three key publications (Fig. 3), clearly revealing an increasing trend of invasions in

**Table 1** Some physiological traits of exotic woody plants that allow establishment, survival, and spread into ecosystems.

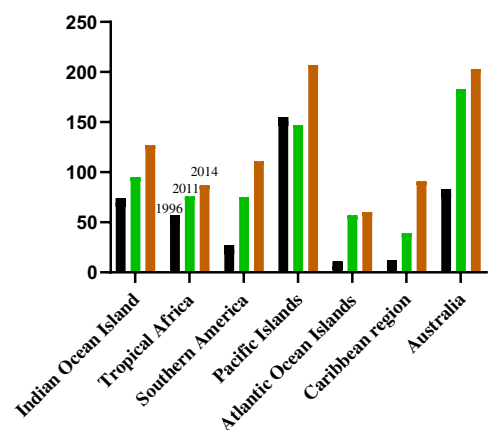
Physiological traits	Invasive woody specie	References
High plasticity	<i>Clidemia hirta</i>	Richardson and Pyšek (2006)
	<i>Schinus terebinthifolius</i>	Spector and Putz (2006)
	<i>Lantana camara</i>	Sharma and Raghubanshi (2011)
	<i>Calotropis procera</i>	Sobrinho et al. (2013)
	<i>Cytisus scoparius</i>	Srinivasan et al. (2007)
Fast growth	<i>Prosopis juliflora</i>	Becker et al. (2016)
	<i>Lantana</i> spp.	Love et al. (2009)
	<i>Mikania micrantha</i>	Rao et al. (2020)
	<i>Mimosa caesalpiniiifolia</i>	Podadera et al. (2015)
	<i>Leucaena leucocephala</i>	Hansted et al. (2016)
High propagule production across their capacity for asexual or sexual reproduction (e.g., seeds, vegetative structures)	<i>Cordia alliodora</i>	Edward et al. (2009)
	<i>Prosopis juliflora</i>	Berhanu and Tesfaye (2006)
	<i>Pongamia pinnata</i>	Sugla et al. (2007)
	<i>Cryptostegia grandiflora</i>	Grice, (1996)
	<i>Spartina alterniflora</i>	Davis et al. (2004)
Tolerance to different environments and climates (e.g., salt-tolerant, drought- tolerant, arid or humid zones, shade)	<i>Dichrostachys cinerea</i>	Shikangalah et al. (2020)
	<i>Lantana camara</i>	Mandal and Joshi (2014a, b)
	<i>Prosopis</i> spp.	Shackleton et al. (2014)
	<i>Leucaena leucocephala</i>	Pandey and Roy (2011)
	<i>Spartina alterniflora</i>	Li et al. (2009)
	<i>Schinus terebinthifolius</i>	Panetta and McKee (1997)
	<i>Senegalia mellifera</i>	Shikangalah et al. (2020)
Capacity of to release allelopathic compounds in the environment	<i>Schinus terebinthifolius</i>	Morgan and Overholt (2005)
	<i>Prosopis juliflora</i>	Getachew et al. (2012)
	<i>Lantana camara</i>	Mandal and Joshi (2014a, b)
	<i>Acacia dealbata</i>	Lorenzo et al. (2013)
	<i>Psidium guajava</i>	Witt et al. (2018)
	<i>Dichrostachys cinerea</i>	Nielsen et al. (2013)
High dispersal capacities (e.g., explosive release of seeds, high viability and longevity of seeds; persistent seed banks)	<i>Ligustrum lucidum</i>	Powell and Aráoz (2018)

all six geographical regions, with Australia and the islands of the Pacific Ocean standing out as areas of highest abundance (Fig. 3).

As noted by Milbau and Stout (2008), it is not possible to put exact numbers on woody plant species invading the tropics, due to the lack of accurate data on exotic flora in most tropical countries, but also because, in the past, there was a deliberate effort by some agencies to promote exotic species to the rest of the world (e.g., Australia promoted *Eucalyptus*, *Acacia*, etc.). For example, some species of the genus *Prosopis*, native to the Americas, have been declared invasive in several regions of Africa and tropical Asia, although its presence has also been reported on the Australian continent and islands in the Pacific Ocean (Al-Assaf et al. 2020). The species *Mikania micrantha* has only been reported as invasive in the humid tropics of the Pacific and Asian countries, including India (Banerjee et al. 2017); however, species such as *Psidium cattleianum*, *Chromolaena odorata*, *Lantana camara*, and *Leucaena leucocephala* have a wider distribution, as they are reported to be invasive in Australia, Africa, and Pacific Ocean islands (Medeiros 2004; Mandal and Joshi 2014a, b; Dhami 2018; Campbell et al. 2019).

The current spread of invasive woody plants is the result of usually a complex mix of factors, and for some species

their current presence in the tropics is due to their horticultural, agricultural, ornamental, or forestry use, favoring their intercontinental trade (Dyer et al. 2019; Meléndez and Rojas

**Number of detected species**

**Fig. 3** Evolution of number of invasive woody species detected in six tropical geographical regions. In the graph, each color represents the year of study (e.g., black column: 1996, green column: 2011, and brown column: 2014). Data compiled from Binggeli (1996), Richardson and Rejmanek (2011), and Rejmanek (2014).

2021). The efforts of many botanical gardens to maximize their collections of exotic species from around the world initiated and stimulated this trade in many tropical regions. For example, Dawson et al. (2008) cited 15 tropical regions in Africa, Australia, the Pacific Islands, and Latin America where the introduction of invasive species occurred through botanical gardens.

More recent research warns about the impact that some socioeconomic factors (e.g., cultural beliefs, financial and educational resources, tourism, and urbanization projects [Westphal et al. 2008; Gudiel et al. 2016; Mukaromah and Imron 2019; Lowry et al. 2020]) are having on the current spread of these invasive species in tropical Pacific Island countries.

In general terms, it can be concluded that the current extent of invasive woody plants in the tropics is very heterogeneous, given the differences in ranges of distribution of species, and the different intensity in the anthropogenic factors acting as drivers of the dispersion.

## 5 Interactions between eradication, containment, and the ecosystem

Invasive woody plant management actions in the tropics have generally been motivated by the threat these plants pose to the biodiversity of impacted ecosystems (Van Wilgen and Richardson 2014). These actions are very diverse and depend on three main factors, namely (1) the characteristics of the invasion itself (e.g., extent, density of the invader, and impact), (2) the physical characteristics of the invaded ecosystem (e.g., topography, texture, effective soil depth), and (3) the human factor (e.g., educational level of the personnel involved, local environmental regulations, availability of equipment, cost of management actions, risk-benefit analysis of each action).

Eradication programs are a set of actions aimed at eliminating all reproductive plants, juveniles, seedlings, and the soil seedbank in affected ecosystems, and have been targeted towards highly invasive species in the tropics, e.g., *Lantana camara* in India (Love et al. 2009), *Miconia* spp. in the Pacific (Perroy et al. 2017), *Falcataria moluccana* in American Samoa and Hawai'i (Hughes et al. 2013), and *Gleditsia triacanthos* in Australia (Csurhes et al. 2004). According to Murugan et al. (2020) citing other authors, complete removal is considered an effective way to sustainably reduce the density of invasive populations and restore ecosystem services, including recovery of native biodiversity. However, such complete removal programs have potential undesirable ecological effects such as soil erosion and further loss of biodiversity and are therefore a matter of much debate related to the cost-benefit analysis, the availability of effective methods of

eradication, and the duration of actions (generally many years) (Brooks and Galway 2008; Meyer 2014; Borges et al. 2018). In fact, total elimination of the invader has never been proven successful, and this is due to a variety of causes, the most important being the presence of persistent seed banks (Gioria et al. 2021). Another reason is the low efficiency of eradication methods in cases of very dense or large populations. Species such as *Olea europaea* L. subsp. *Cuspidata* (Cuneo et al. 2010) and *Dichrostachys cinerea* (Wakeling and Bond 2007) combine both strategies: highly persistent seed banks and the formation of very dense populations. Finally, it has also been shown that climate change may further increase the risk of expansion, rendering eradication or control attempts more difficult (Bradley et al. 2009). Therefore, given that complete eradication of invasive woody species has proven extremely difficult, if not impossible, efforts should be directed towards mitigation strategies that minimize risks of damage to the overall ecosystem while maximizing the potential benefits of the invasive species.

Even though complete eradication of invasive species is impractical, according to Renteria et al. (2012), unintended effects on native species resulting from control efforts and off-target effects may outweigh the conservation benefits of eradication. As an alternative to complete eradication, invasive species may also be contained to a level where the ecosystem can recover, also minimizing negative impacts of eradication methods (herbicide use, bulldozing) on the ecosystem by using less disruptive management strategies. For example, the use of co-evolved natural enemies has been shown to be an option in cases where the introduced natural enemy is not a pest to native vegetation (Ngondya et al. 2016; Shen et al. 2018). The effectiveness of this method depends on factors such as (i) density of the invasive woody species, in that a biocontrol agent will be less efficient where the plant reaches its highest densities (Swope et al. 2017); (ii) range of the biological agent's hosts (e.g., biological agents with a wide range of hosts will affect multiple species in the ecosystem); and (iii) the high costs associated with the application of commercial or imported biological control agents (Shackleton et al. 2014). However, this type of practice has been successful in containing some highly invasive species in several cases, with containment levels sometimes exceeding 50% (Table 2).

Given that alternatives such as introduction of biological control agents generate variable responses in invasive woody species, control measures for invasive woody species should ideally be combined with harnessing their potential benefits. In the next section, we provide a detailed overview of potential key benefits of invasive woody species, with the emphasis on effects on soil, given that soil is the basis for the provisioning of most ecosystem services.



**Table 2** Management of some invasive woody plants by biological control in tropical countries.

Region	Invasive woody specie	Biological control agents	Outcome	References
Papua New Guinea	<i>Mimosa invisa</i>	Psyllid, <i>Heteropsylla spinulosa</i>	Decline of infestation from 100% in 1991 to less than 5% in 2 years following the release of the psyllid	Kuniata and Korowi (2004)
Australia	<i>Leucaena leucocephala</i>	Bruchid, <i>Acanthoscelides macrophthalmus</i>	Seed predation of <i>L. leucocephala</i> by <i>Acanthoscelides macrophthalmus</i> ranged from 10.75 to 53.54%	Raghu et al. (2005)
Australia	<i>Mimosa pigra</i>	<i>Carmentis mimosa</i>	Decrease of Mimosa seed rainfall by 90% at the highest densities of the biological control agent	Paynter (2005)
India and Pacific Islands	<i>Mikania micrantha</i>	Fungus, <i>Puccinia spegazzinii</i>	Variable effectiveness percentage depending on the collection site of the biological agent	Day et al. (2016) Ellison et al. (2008)
Australia	<i>Acacia nilotica</i>	Leaf-feeding geometrid, <i>Chiasmia assimilis</i>	Decrease in the number of leaves by 97%, surface biomass by 87%, and underground biomass by 77%.	Lockett et al. (2012)
Brazil	<i>Miconia calvescens</i>	Wasp, <i>Allorhogas</i> sp. and beetle, <i>Apion</i> sp.	Both <i>Apion</i> and <i>Allorhogas</i> infestations resulted in 62% and 79% fewer seeds in infested fruits than healthy fruits, respectively	Badenes-Perez and Johnson (2007)
China	<i>Ligustrum sinense</i>	Bea beetle, <i>Argopistest sekooni</i>	The observed defoliation percentages ranged from 20 to 48%	Zhang et al. (2008)
South Africa	<i>Tecoma stans</i>	Flea beetle, <i>Heikertingerella</i> sp.	97% of leaves damaged	Madire et al. (2021)
Brazil	<i>Tecoma stans</i>	Leaf roller, <i>Eulepte</i> spp. mite <i>Tetranychus ludeni</i>	Heavy infection at field level. Evidence of defoliation and killing off <i>T. stans</i> seedlings with <i>Tetranychus ludeni</i>	Vitorino et al. (2004)

## 6 Invasive woody plants a promoter of services to the agricultural sector

Despite the often-considerable damage caused by invasive woody species to the ecosystem, a paradigm shift is taking place in many tropical countries regarding them, namely from full eradication to control in combination with maximizing potential benefits. Potential benefits include biomass generation for energy production (e.g., *Dichrostachys cinerea* [Gutiérrez et al. 2018] and *Tamarix* spp. [Nielsen et al. 2011]), provisioning of bio-active and medicinal compounds (e.g., *Prosopis juliflora* [Idris and Abdel-Rahim 2018] and *Mimosa pigra* [Tamiliarasi and Ananthi 2012]), protection of degraded soils against further degradation, fodder production, soil C sequestration, and restoration of soil fertility. These benefits thus all relate either indirectly or directly to the agricultural sector, and we will highlight here the two most prominent examples, namely animal fodder

production and contribution to soil quality with a greater focus on the latter.

### 6.1 Contribution to animal fodders and associated risks

Despite the undesirable effects that some species with invasive potential can have when used in animal feed, due mainly to the presence of secondary compounds (e.g., alopecia, weight loss, toxicity [Aro et al. 2009; De Angelis et al. 2021]), they are widely used by farmers in the tropics. In this way, locally available resources can be utilized while achieving some effectiveness in invasion management (Shackleton et al. 2019a, b; Ravhuhali et al. 2021). The inclusion of species such as *Dichrostachys cinerea*, *Prosopis* spp., *Leucaena leucocephala*, and *Chromolaena odorata* in the diets of local livestock (e.g., dwarf fallow deer [Oni et al. 2020], pigs [Martín et al. 2017], broilers [Jiwuba et al. 2018], goats

[Rubanza et al. 2007]) has been the result of research to unravel their medicinal and nutritional qualities. Low animal productivity in the tropics is often related to animal health status as well as to the low nitrogen and high fiber content of the local plant species and crop residues that constitute the base ingredients of most animal rations adopted by small-holder farmers. Particularly, local availability of protein-rich feed resources is challenging, albeit essential livestock feeding in a context of sustainable intensification. Nutritional needs of animals depend on their physiological status (e.g., body weight, growth rate, lactation, pregnancy) and external factors (e.g., expenditure for movement, labor, heat stress). Although protein requirements are expressed as net or metabolizable protein, heuristic dietary crude protein standards are often used. As such, dietary crude protein content required for maintenance could be estimated between 45 and 65 g crude protein/kg dry matter while growing or lactating animals require between 85 and 125 g crude protein/kg dry matter and 110 to 160 g crude protein/kg dry matter, respectively, depending on the physiological stage and production rates as well as the digestibility of the feed resources (McDonald et al. 2011). Many invasive woody plant species, especially from the Fabaceae family, have a higher crude protein content than tropical grasses (Table 3) and as such could be considered a valuable local protein source.

Despite, invasive woody may affect grass production (e.g., *Dichrostachys cinerea* and *Terminalia sericea* [Randle et al. (2018)]); other authors have shown the benefits of these species within an animal nutrition context. Indeed, a tolerable level of invasion, especially if leguminous species are involved, can (i) promote forage production in certain cases, both in terms of richness of native woody species and forage biomass (Tecco et al. 2006; Lüscher et al. 2014) and (ii) compensate for more than 50% of forage lost because of displacement of herbaceous species present before the invasion (Ndhlovu et al. 2011). For

example, Ancira et al. (2006) cited a study in which up to 70% more forage species (not detailing whether the increase corresponds to biomass or diversity) were obtained under a *Prosopis leavigata* mesquite canopy than in open areas. Hölscher et al. (2005) found that woody vegetation in abandoned crop fields usually has a higher species diversity than vegetation in abandoned pastures. Therefore, an ecosystem invaded by woody plants could represent a benefit for livestock systems if managed appropriately, certainly if one considers that there are some highly degraded areas where any woody vegetation would be better than none (Table 4).

## 6.2 Impact of the invasive woody plant on soil properties and functions

Many soils in the tropics are inherently infertile because of advanced weathering, often combined with soil degradation, and characterized by low levels of organic matter and nutrients (Nair 2019). Invasions of woody plants into ecosystems (e.g., savannahs or forests) can be considered a symptom of ecosystem degradation caused by unsustainable exploitation, land use change, and fragmentation. However, new studies indicate that many species are promoters of positive changes in host ecosystems when these are seriously affected by degradation processes, low natural fertility, or compaction (Domínguez et al. 2016). For example, invasive species can help to recover physical soil properties and facilitate the restoration processes in degraded areas where the native species failed to colonize (Vasquez-Valderrama et al. 2020) (Table 5).

The effects on soil can be opposite depending on the species. For example, *Mimosa pudica*, *Berberis thunbergii*, and *Rhamnus cathartica* can increase soil pH because of their high nitrate absorption rates (Ehrenfeld et al. 2001; Heneghan et al. 2006; Wang et al. 2015a, b), while others such as *Dichrostachys cinerea*, *Myrica micrantha*, and

**Table 3** Crude protein content of some invasive woody species and tropical forage species.

Species name	Family	Plant parts	Crude protein (%)	References
<b>Invasive woody species</b>				
<i>Prosopis juliflora</i>	Fabaceae	Pods	18.5	Koeh et al. (2010)
<i>Acacia farnesiana</i>	Fabaceae	leaves	15–24.2	Dynes and Schlink (2002)
<i>Leucaena leucacepha</i>	Fabaceae	leaves	23.7	Mataveia et al. (2019)
<i>Dichrostachys cinerea</i>	Fabaceae	leaves	17.8	Madibela et al. (2004)
<i>Mikania micrantha</i>	Asteraceae	Whole plant	18	Lalhuthangi and Buragohain (2020)
<i>Calliandra calothyrsus</i>	Fabaceae	Whole plant	16.8	Mabeza et al. (2018)
<b>Tropical forage species</b>				
<i>Heteropogon contortus</i>	Poaceae	Whole plant	2.57	Panjaitan et al. (2010)
<i>Digitaria eriantha</i>	Poaceae	Whole plant	7.55	Panjaitan et al. (2010)
<i>Pennisetum purpureum</i>	Poaceae	Whole plant	11	Kambashi et al. (2014)
<i>Urochloa ruziziensis</i>	Poaceae	Whole plant	10.1	Kambashi et al. (2014)
<i>Macrotylom aaxillare</i>	Fabaceae	Whole plant	12.1	Lista et al. (2019)

**Table 4** Estimated annual contribution to soil N supply by N fixation in invasive (N-fixing) woody species. (\*): ranges of N returned to the soil according to invasion time. In the case of *Morella cerifera*, 37 kg

N ha<sup>-1</sup> year<sup>-1</sup> corresponds to thicket of 60 years and 118 kg N ha<sup>-1</sup> year<sup>-1</sup> corresponds to thicket of 20 years.

Species	Soil total N (kg N ha <sup>-1</sup> year <sup>-1</sup> )	Location of study	References
<i>Acacia mangium</i>	40	<i>Eucalyptus</i> plantations	Voigtlaender et al. (2019)
<i>Acacia mangium</i>	65	Field with a monoculture of <i>Acacia mangium</i>	Voigtlaender et al. (2019)
<i>Acacia dealbata</i>	40	<i>Eucalyptus regnans</i> forest	May and Attiwill (2003)
<i>Robinia pseudoacacia</i>	86	<i>Robinia</i> -invaded stands	Rice et al. (2004)
<i>Robinia pseudoacacia</i>	75	<i>Robinia</i> -invaded stands	Boring and Swank (1984)
<i>Calliandra calothyrsus</i>	31	Field with a monoculture of <i>Calliandra calothyrsus</i>	Gathumbi et al. (2002)
<i>Prosopis juliflora</i>	59	Reclaimed coal mine soil after forestation with <i>Prosopis</i>	Ahirwal et al. (2017)
<i>Cytisus scoparius</i>	17	<i>Pinus radiata</i> plantation	Watt et al. (2003)
<i>Ulex europaeus</i>	26	Field with mixed-species plantations	Skeffington and Bradshaw (1980)
<i>Leucaena leucocephala</i>	149	Field with mixed-species plantations of <i>Leucaena</i> and <i>Megathyrsus maximus</i>	Sarabia et al. (2020)
<i>Morella cerifera</i> *	37-118	Shrub thickets interspersed with dunes and relic grasslands	Brantley (2009)

*Prosopis juliflora* show a tendency to decrease soil pH (El-Keblawy and Al-Rawai 2007; Steinlein 2013). The presence of *Juniperus virginiana* increased soil moisture as compared to its absence (Pierce and Reich 2010), while *Chromolaena odorata* invasion has been associated with reduction of available soil moisture due to its high transpiration rates (te Beest et al. 2017).

### 6.2.1 Impact on soil microbial communities

Soil microorganisms are the catalysts for many reactions occurring in soil and their activities are decisive for most, if not all, chemical and physical soil processes, including

the functions of nutrient mineralization, and stabilization (and mineralization) of organic C. Through their intimate interactions with plant roots, they also crucially determine plant growth and plant health (Torres et al. 2021). Despite considerable redundancy in the soil microbial community, changes in the microbial community structure are thus likely to affect these processes and to modify the overall functioning of the soil (Vallejo et al. 2012). Therefore, understanding these changes following land use change or changes to land management can help us make science-based decisions to select land management practices that enhance ecosystem sustainability (Acosta et al. 2010; Vallejo et al. 2012).

**Table 5** Contribution of some pioneer woody species to SOC sequestration after afforestation. (\*) initial value taken from another study in the same area (Adman et al. 2020), (\*\*) value taken from undisturbed nearby native forest.

Pioneer woody species	Evolution of SOC in different afforestation programs (%)		Study site	Soil depths (cm)	References
	SOC before afforestation	SOC after afforestation			
<i>Robinia pseudoacacia</i> (after 15 years)	0.72	1.02	Afforested cropland, China	0–20	Liu et al. (2018)
Mixed plantations of <i>Acacia mangium</i> and <i>Paraserianthes falcataria</i> (after 9 years)	0.09*	1.79	Coal mine, Indonesia	0–10	Woodbury et al. (2020)
<i>Prosopis juliflora</i> (after 22 years)	0.07	0.69	Afforested sand dunes, Iran	0–5	Moradi et al. (2017)
	0.04	0.07		5–50	
Mixed plantations of <i>Acacia nilotica</i> , <i>Albizia lebbek</i> , <i>Dalbergia sissoo</i> , <i>Eucalyptus</i> hybrid, and <i>Prosopis juliflora</i> (after 13.5 years)	0.08	0.55	Common land in salt affected wastelands in semi-arid hills, India	0–15	Pal and Sharma (2001)
	0.06	0.46		15–30	
	0.06	0.39		30–45	
<i>Prosopis juliflora</i> (after 8 years)	1.29**	0.89	Reclaimed coal mine soil in India	0–20	Ahirwal et al. (2017)
	0.43**	0.32		20–40	
	0.20**	0.12		40–60	

Ecosystems invaded by woody plants are considered disturbed ecosystems, so soil microbial communities can also be expected to respond to these changes. Invasive woody plants may interrupt interactions between soil communities and native plants. For example, Kaushik et al. (2021) demonstrated that the co-occurring native and invasive *Prosopis* species have significantly different rhizosphere bacterial communities in terms of composition, diversity, and their predictive metabolic potentials. In addition, these researchers demonstrated that the rhizosphere microbiome of invasive *Prosopis* offers it a fitness advantage and influences invasion success of the species. The microbial community in invaded soils is modified through two pathways, (1) litter effect through modifications of detritus inputs and the physical soil environment, combined with rhizosphere effects through changes in root exudation and (2) direct root-biota interactions (Zhang et al. 2019), leading to positive or negative feedback mechanisms with the invasive species. The positive interactions include symbiotic associations with beneficial microbes, such as mycorrhiza and plant growth promoting rhizobacteria (PGPR). Negative interactions mostly include antimicrobial effect (Wu and Yu 2019).

For example, in sites invaded by woody legumes such as *Prosopis*, *Leucaena leucocephala*, and *Mimosa* species, interactions with native rhizobia and AMF (arbuscular mycorrhizal fungi) facilitated the establishment of the woody legumes in new habitats and made it a stronger competitor than native plant species (Mahdhi et al. 2019). In addition,

Vilá et al. (2011), in a study comprising 202 tree species, demonstrated that one of the impacts of alien plants into ecosystems is the increase in soil microbial activity. In most cases, the positive feedback between invasive species and microbial activity is mediated by microbial enzymes (Bandick and Dick 1999; Neina 2019), the production of which is a function of the concentration and the quality of nutrients within the ecosystem (Allison et al. 2007).

Table 6 summarizes thirteen studies reporting on the impact of invasive woody species on 6 of the main soil enzymes. Overall, invasive woody species tended to increase (36 cases) rather than decrease (7 cases) enzyme activities, but importantly also the direction of the impact on soil enzyme activity sometimes differed between studies (e.g., *Lantana camara* in southern China and central India), demonstrating that the invader-soil interaction is environment-specific.

### 6.2.2 Soil nutrient and carbon content

In general terms, vegetation may alter the soil nutrient and carbon content by a variety of mechanisms. Direct effects are due to net inputs of C and N by litter, root exudates, dead roots, and fixation of atmospheric N. But changes in vegetation can have many indirect effects on dynamics and thus stocks of C and nutrients, by, e.g., altering the mineralization rate of soil organic matter, by affecting the local hydrology and thus the rates of leaching/capillary rise, run-off, and

**Table 6** Impact of invasive woody species on some soil enzyme activities in tropical regions. *Dh*, dehydrogenase; *β-G*, *β*-glucosidase; *Ure*, urease; *acid Ph*, acid phosphatase; *alka Ph*, alkaline phos-

phatase; *Cat*, catalase; *Cell*, cellulase. *NA.*, not analyzed; 0: no differences; increase: +; decrease: -

Region	Invasive woody specie	Outcome							References
		<i>Dh</i>	<i>β-G</i>	<i>Ure</i>	<i>Ph</i>		<i>Cat</i>	<i>Cell</i>	
					<i>Acid</i>	<i>alka</i>			
China	<i>Lantana camara</i>	NA	NA	+	+	+	NA	+	Fan et al. (2010)
Hawaii	<i>Falcataria moluccana</i>	NA	+	+	+	NA	NA	NA	Allison et al. (2006)
China	<i>Mimosa pudica</i>	NA	NA	+	+	NA	+	+	Wang et al. (2015a, b)
Philippines	<i>Acacia</i> spp.	+	NA	NA	+	+	NA	NA	Lee et al. (2006)
China	<i>Mikania micrantha</i>	NA	+	+	NA	NA	NA	NA	Li et al. (2006)
China	<i>Eupatorium adenophorum</i>	NA	0	+	+	0	NA	0	Sun et al. (2013)
Ivory Coast	<i>Chromolaena odorata</i>	NA	+	NA	+	+	NA	NA	Koné et al. (2021)
China	<i>Chromolaena odorata</i>	NA	NA	+	+	NA	0	NA	Xu et al. (2020)
India	<i>Lantana camara</i>	-	-	NA	-	+	NA	NA	Singh et al. (2018)
India	<i>Prosopis juliflora</i>	-	NA	-	NA	NA	NA	NA	Murugan et al. (2020)
	<i>Acacia mearnsii</i>	+	NA	+	NA	NA	NA	NA	
Taiwan	<i>Phyllostachys edulis</i>	NA	NA	-	0	0	NA	-	Chang and Chiu (2015)
China	<i>Lantana camara</i>	NA	NA	+	NA	NA	+	+	Wang et al. (2015a, b)
Shenzhen China	<i>Mikania micrantha</i>	0	+	NA	+	NA	NA	NA	Sun et al. (2019)
Huizhou China		+	+	NA	+	NA	NA	NA	
Guangzhou China		0	+	NA	0	NA	NA	NA	

erosion, or even by influencing patterns of atmospheric deposition (by changes in canopy surface roughness, Hartanto et al. 2003). Also, changes in rooting depth may cause a redistribution of plant nutrients from deep in the soil profile to the topsoil, effectively increasing nutrients in superficial soil layers. Importantly, vegetation changes can also strongly affect the distribution of soil nutrients between plant available and unavailable forms. For example, soil P fractions and P fluxes can be greatly influenced by vegetation restoration types (Fu et al. 2020).

**Effects of invasive woody species on SOC** As explained above, disturbance of ecosystems, whether anthropogenic or natural, leads to changes in biogeochemical processes. Soil carbon is the element on which the entire food chain depends, controlling the hydrological, biological, and chemical functioning of the soil (Abbas et al. 2020).

Currently, the potential of agricultural systems to sequester atmospheric CO<sub>2</sub> as a means of mitigating greenhouse gas emissions is an important research priority (Conrad et al. 2017) and C sequestration could be one of the potential benefits of invasive woody species (Nelson et al. 2008; Blaser et al. 2014; Birhane et al. 2017). According to some studies, dominant plant species may regulate the soil C sequestration potential in ecosystems (Makkonen et al. 2012; Tamura and Tharayil 2014) and therefore the changes in SOC content. For example, Li et al. (2016) demonstrated that SOC content decreased significantly with shrub encroachment by the genera *Acacia* and *Chucairaga* but increased significantly with encroachment by the genera *Juniperus*, *Myrica*, *Prosopis*, and *Quercus*. This is attributed to factors such as the root turnover of the species, the volume of litter deposited (Andivia et al. 2016), the abundance of recalcitrant compounds in the biomass (e.g., lignocellulosic complex [Hinman et al. 2019]), and functional traits of the plants such as their rapid growth (De Deyn et al. 2008), and the ability to fix atmospheric nitrogen (e.g., invasive nitrogen-fixing woody species increase root mass more frequently than other species in order to fix N more efficiently, and this increased root mass in turn increases soil carbon sequestration).

For example, afforestation (conversion of cropland or marginal land to forest) is considered one of the key climate change mitigation strategies because of its potential for carbon sequestration (Arora and Montenegro 2011; Doelman et al. 2020). According to Yosef et al. (2018), the effectiveness of afforestation as a climate change mitigation strategy depends on the balance of the biogeochemical and biogeophysical effects and was shown to be most effective in the tropics, where water availability enhances carbon uptake. The selection of the species to be planted is not an arbitrary process, but follows a series of regulations

including the type of woody plants (Ladegaard et al. 2005) or their potential environmental benefits (e.g., amounts of C lost or gained by the soil, C accumulation in tree biomass), economic viability, the level of adaptation of the species to the degraded ecosystem (e.g., survival rate) and its physiological characteristics (e.g., fast-growing), previous land use, and the climate of the region (Semenyutina et al. 2018). So invasive species in this case would be deliberately planted if their perceived benefits for C sequestration would outweigh their potential invasion risk (Ewel et al. 1999). Paul et al. (2002) highlighted a number of benefits for soil of such deliberate introduction: (i) the soil carbon gain is higher when using N-fixing species on ex-cultivated land in tropical or subtropical regions compared to temperate zones, (ii) the amounts of soil carbon start to recover or may even reach almost the level prior to deforestation a few decades following plantation establishment. (e.g., between 20 and 50 years of forest rotations, Paul et al. 2002; Lemma et al. 2006), (iii) there is an uneven distribution of soil carbon gains, the gains being higher in the top 10 cm of soil compared to deeper layers, (iv) the amounts of C lost or gained by the soil are generally small compared to the accumulation of C in tree biomass.

In the same way that Paul et al. (2002) and Lemma et al. (2006) express a range of years for the results of reforestation programs with woody species to be manifested in the recovery of SOC, the variability in range of years for SOC recovery to be manifested is also evident from Table 5. In general, these reforestation programs have led to SOC gains in the topsoil layers when bare soil is taken as a reference. However, the SOC levels of these reforested ecosystems may not exceed or equal the SOC values of the original ecosystem. Therefore, the number of years between the start of reforestation and the measurement of the SOC level will largely determine the results of such assessments. Another important aspect is that the SOC gain decreases with the depth at which the survey is conducted and is strongly determined by the botanical composition of the reforested site (mixed or simple plantations).

Despite the positive impact of invasive woody species on soil carbon storage and conservation, we do not believe it is possible to justify their introduction without first examining the specifics of each region and the risk-benefit ratio. For example, in India, the highly invasive species *Dichrostachys cinerea* is being evaluated for its high natural regeneration capacity for soil conservation in arid areas, gully reforestation, and dune stabilization (Bohra 2010). However, this approach could not possibly be implemented in Cuba because the high natural regeneration capacity of *Dichrostachys cinerea* there has resulted in the loss of large areas of arable land.

**Influence of invasive woody plants on the soil nitrogen stocks** Nitrogen is a major limiting factor for agricultural productivity in many parts of the tropics (e.g., Indonesia [Hanisch et al. 2011], Cuba [Lok et al. 2019], Sub-Saharan Africa [Vanlauwe et al. 2017]), and the question has arisen how land use history has impacted nitrogen dynamics in a context of climate change and what the implications are for the ecosystem in the short, medium, and long term. Plant species influence N cycling in the ecosystem in direct and/or indirect ways, such as alterations in N use efficiency, changes in soil microbial community, changes in litter decomposition rates, and N inputs and losses as well as by alterations in physicochemical soil properties (Boutton and Liao 2010; Wang et al. 2015a, b).

The impact of invasive woody plants on soil nitrogen reserves can be explained through (i) the relationship that these species establish with the other biotic and abiotic elements of the ecosystem (e.g., soil microbial communities, associated vegetation, soil chemical composition) or (ii) the legacy of these species in the soil after their removal. For example, some studies in which invaded areas have been managed to establish silvipastoral systems where both invasive  $N_2$ -fixing species and indigenous non- $N_2$ -fixing species coexist, have shown that the amount of nitrogen that is entering into the soil is higher compared to monoculture systems. In fact, these mixed systems are an attractive option to improve the long-term soil N status in fast-growing plantations established in tropical soils (Voigtlaender et al. 2019). Examples of such systems are *Robinia pseudoacacia*-*Pinus tabulaeformis* (Yuan et al. 2017), *Eucalyptus*-*Acacia dealbata* (May and Attiwill 2003), *Eucalyptus*-*Acacia mangium* (Voigtlaender et al. 2019), *Lantana camara*-*Dichrostachys cinerea* (L.) (Mahla and Mlambo 2019), and *Leucaena leucocephala*-*Megathyrsus maximus* (Sarabia et al. 2020). The increase in nitrogen availability in mixed-species plantations with a nitrogen-fixing species is related to (1) fixed N that may become available to non- $N_2$ -fixing species after plant and microbial tissues die and decompose, releasing N that cycles through the ecosystem; (2) via root exudation or mycorrhizal connections between root systems when both species form symbioses with the same mycorrhizae, and (3) reduced or no competition for N by the  $N_2$ -fixing plant because of its reliance on its own fixed N, which may have a share from 10% to almost 100% of its N uptake (Forrester et al. 2007) and Tchichelle et al. 2017). Variation in soil N availability because of the activity of invasive woody species has been reported in several studies (Table 4).

Invasive woody species also leave a legacy that impacts soil nitrogen availability even after their complete removal. According to Prior et al. (2018) and Nsikani et al. (2018), one of the most important aspects after the clearing of the invasive woody plant is the high soil N content and

availability, which can persist and even temporarily increase with the decomposition of the residual biomass of the invasive plants. However, there is little information on the evolution of this availability over time, and the few studies that explored this issue did not cover the same time frames. For example, Grove et al. (2015) reported an increase in nitrogen availability 1 month after the complete removal of *Cytisus scoparius* compared to intact *C. scoparius* control plots, but after 10 months the N availability had decreased (70% less) in the removal plots compared to the invaded state. On the other hand, Katz et al. (2020) found that 1 year after *Elaeagnus angustifolia* removal, soil N levels were greater than in plots without removal. Such information is crucial when these soils need to be taken into production again, and therefore there is a need for more in-depth research on this topic.

**Impact on soil phosphorus** Phosphorus is a critical plant nutrient and is often the main limiting nutrient for biomass production in tropical settings, especially in highly weathered tropical forest soils (Aleixo et al. 2020). Natural soil phosphorus reserves are the result of geological processes and soil formation and cannot be altered by changing vegetation. The availability of P, however, can be extremely low in soils even at relatively high total P levels because of strong binding mechanisms, which in tropical soils of low pH are mainly due to strong fixation by pedogenic Fe, Al, and Mn (oxy-)hydroxides. Also, in soils that have received P fertilizer in the past, this P is rapidly rendered unavailable by such fixation reactions.

The impact of woody invasions on soil P availability is variable. The analysis must start from the fact that invasive woody plants can colonize both environments with low levels of available P and environments with high availability. In either case, the subsequent impact will depend on the characteristics of the invasive species and how it interacts with the local soil conditions (e.g., the microbial community, texture, and chemical properties of the soil). For example, Kerr and Ruwanza (2016) reported higher soil P availability under *Eucalyptus grandis* invasion (14.5 mg kg<sup>-1</sup>) compared to cleared (3.8 mg kg<sup>-1</sup>) and natural (6.8 mg kg<sup>-1</sup>) sites. These researchers suggested that the differences in P availability were due to the lower soil pH in the cleared and natural areas (pH 4.7 and 3.4, respectively) compared to the invaded soil (pH 4.9). At such low pH, there is strong P fixation to Al and Fe compounds.

On the other hand, it has been shown that the introduction of some nitrogen-fixing species (e.g., acacias) can lead to long-term soil P limitation (Koutika et al. 2016). This fact has been associated to the higher extraction of available P in the soil due to the higher uptake of this element. Also, in ecosystems with invasive nitrogen-fixing species, increases in soil enzyme activities related to mineralization

(e.g., acid, and alkaline phosphomonoesterases, phytases, and nucleotidases) have been observed, which help to meet the high P demands of N fixation (Zhou and Staver 2019; Wei et al. 2019). Enzyme upregulation is directly related to the microbial community present in the rhizosphere of these plants (e.g., phosphorus solubilizing fungi) and is one of the mechanisms contributing to their successful establishment and spread (Zhang et al. 2021).

Soil phosphorus availability is also influenced by the density of the invader in the ecosystem. For example, Zhang et al. (2020) observed that soil P availability was slightly reduced at relatively low densities (25–50%) of the invader. However, once the environment becomes dominated by the invader (invasion levels of 75–100%), P availability returned to levels equal or higher than those observed in the non-invasion stage (0%). This fact was also reported by Lorenzo et al. (2010) in areas with partial cover of *Acacia dealbata*, areas dominated by this species and non-invaded areas. In this case, exchangeable P decreased in areas with partial cover of *A. dealbata* compared to non-invaded areas but increased considerably in areas dominated by the invasive plant, reaching values much higher than those observed in non-invaded areas. Considering that P is often the most limiting nutrient in the soil, knowing how its availability fluctuates with different factors is crucial to implement effective management strategies. Therefore, proper management of the invasion (e.g., considering edaphoclimatic conditions of the invaded ecosystem as well as the density and type of stand present) could make a difference in terms of reaping the benefits of these plants. This density effect on P clearly demonstrates that the balance between maximizing the benefits of invasive woody species and controlling these species is very delicate, given that in areas where they become dominant control is much more difficult.

### 6.2.3 Impacts on the soil water cycle

Soil water content influences a large variety of plant biophysical processes (Bittelli 2011), and therefore, analyzing the impacts of soil hydrology on plant invasions and vice versa is key to implementing effective management strategies. According to Cavaleri et al. (2014), citing other authors, woody invasives can greatly impact the water balance of a system, as woody plants generally have higher rainfall interception, higher transpiration rates, deeper roots, greater standing biomass, greater carbon sequestration, and longer growing seasons than co-occurring herbaceous plants. However, impacts of these species on soil water reserves can also depend on environmental factors (e.g., type of biome, seasonality, physical soil properties, density of vegetation, and its functional traits).

For example, Wilcox (2002) noted woody vegetation may alter both surface and subsurface streamflow generation, with the relative abundance of vegetation determining the extent of alteration.

Some invasive woody species can colonize and expand without difficulty in ecosystems severely affected by water stress (e.g., *Leucaena leucocephala* [Honda et al. 2018], *Tamarix ramosissima* [Cleverly et al. 1997], *Acacia mearnsii* [Crous et al. 2012]), or colonize primarily floodplain wetlands with shallow groundwater tables (e.g., *Prosopis* [Ayanu et al. 2015]). According to Fravolini et al. (2005), the interaction between rainfall and soil texture may lead to differential acquisition and use of seasonal precipitation by mesquite trees (*Prosopis velutina* Woot.) across the landscape. On the other hand, Hennessy et al. (1985) found that *Prosopis glandulosa* dune soils stored water less efficiently than interdune soils. However, Odindi and Kakembo (2011) showed that the surface of the area invaded by certain woody species may have greater moisture retention than the bare inter-shrub area. The variation in soil water reserves in invaded sites also determines the magnitude of certain processes such as biological nitrogen fixation. For example, Dudley et al. (2014) reported that rates of N fixation and productivity by invasive woody legumes may be relatively high where groundwater is abundant and available and severely constrained where it is not.

The removal of invasive woody plants also causes differential impacts on the water cycle. For example, although the removal of these species generally disrupts the hydrological connectivity created in the invaded area (shrub islands), causing further water loss (Okin et al. 2015). According to Dzikiti et al. (2013) impacts on stream flows and groundwater levels following invasive vegetation removal may differ by biome type. Citing other research, they noted that some studies in humid environments reported increased stream flows and groundwater levels following the removal of invading vegetation (e.g., *Acacia mearnsii* and *Acacia longifolia* [Prinsloo and Scott 1999]), whereas other studies in more arid regions reported that decreases in evapotranspiration due to alien vegetation clearing did not translate to increased stream flow (Hart et al. 2005; McDonald 2010) or increased groundwater levels (Hays 2003).

In summary, the impact of invasive woody plants on the soil water cycle strongly depends on environmental factors and functional traits of these species, leading to increases or decreases in soil water reserves. However, when these species are used in the rehabilitation of highly degraded areas (e.g., reforestation plans or programs for the containment of water erosion), they improve the hydrological properties of the soil compared to bare soil, demonstrating again the context dependency of the effects.

**Table 7** Controversies and knowledge gaps in some aspects of the study of the invasive woody plants. Principal knowledge gaps, (1) lack of accurate data of exotic flora in most tropical ecosystems, which could contribute to misestimations on the real invasion extensions in such regions; (2) there is little information on the evolution of soil nitrogen content and its availability over time after complete removal of invasive woody species; and (3) there is little evidence of the success of the eradication and/or containment programs in the long term, considering the changing features of ecosystems, modulated by socioeconomic and climate change aspects.

Points of analysis	Controversies or conflicting issues	References
Role of disturbances in the invasion process	<ol style="list-style-type: none"> <li>1. Exotic woody plants become invasive only when the ecosystem becomes disturbed.</li> <li>2. Exotic woody plants become invasive irrespective of disturbances in the ecosystem.</li> </ol>	<ol style="list-style-type: none"> <li>1. Sakai et al. (2001); Negi et al. (2019)</li> <li>2. Sheil et al. (2000); Durand and Goldstein (2001a, 2001b); Peters 2001; Gurrlich et al. (2005); Martin et al. (2009)</li> </ol>
Eradication or containment	<ol style="list-style-type: none"> <li>1. Complete removal is considered an effective way to reduce the density of invasive populations (e.g., <i>Lantana camara</i> in India, <i>Miconia</i> spp. in the Pacific, <i>Falcataria moluccana</i> in American Samoa and Hawaii, <i>Glodisia triacanthos</i> in Australia).</li> <li>2. Invasive plant species removal programs have potential undesirable ecological effects on soil erosion and biodiversity.</li> </ol>	<ol style="list-style-type: none"> <li>1. Csurhes et al. (2004); Love et al. (2009); Hughes et al. (2013); Perroy et al. (2017); Murugan et al. (2020);</li> <li>2. Brooks and Galway (2008); Meyer (2014); Borges et al. (2018)</li> </ol>
Impact on general soil quality	<ol style="list-style-type: none"> <li>1. Both free grazing and exclusion grazing have the same impact on soil pH.</li> <li>2. Free grazing significantly improves soil pH compared to exclusion grazing.</li> <li>3. Some species can increase soil pH because of their high nitrate absorption rates (e.g., <i>Mimosa pudica</i>, <i>Berberis thunbergii</i>, <i>Rhamnus calhartica</i>).</li> <li>4. Some species show a tendency to decrease soil pH (e.g., <i>Myrica micrantha</i>, <i>Prosopis juliflora</i>, <i>Ulex europaeus</i>, <i>Acacia dealbata</i>, and <i>Robinia pseudacacia</i>).</li> </ol>	<ol style="list-style-type: none"> <li>1. Lu et al. (2015)</li> <li>2. Futa et al. (2017)</li> <li>3. Ehrenfeld et al. (2001); Heneghan et al. (2006); Wang et al. (2015a, 2015b).</li> <li>4. El-Keblawy and Al-Rawai (2007); Steinlein (2013); Souza et al. (2015); Bateman and Vitousek (2018); Lazzaro et al. (2018)</li> </ol>
Soil water impact	<ol style="list-style-type: none"> <li>1. The removal of invading vegetation leads to increased stream flows and groundwater levels (e.g., <i>Acacia mearnsii</i> and <i>Acacia longifolia</i>).</li> <li>2. The removal of invading vegetation does not necessarily result in increased stream flow or groundwater levels.</li> <li>3. Some invasive species can increase soil moisture content compared with adjacent area non-invaded (e.g., <i>Juniperus virginiana</i>)</li> <li>4. Some invasive species can decrease soil moisture content due to its high transpiration rates (e.g., <i>Chromolaena odorata</i>)</li> </ol>	<ol style="list-style-type: none"> <li>1. Prinsloo and Scott (1999)</li> <li>2. Hays (2003); Hart et al. (2005); McDonald (2010)</li> <li>3. Pierce and Reich (2010); Odindi and Kakembo (2011).</li> <li>4. Cavaleri et al. (2014); te Beest et al. (2017)</li> </ol>
Contribution to animal fodders	<ol style="list-style-type: none"> <li>1. The foliage of some invasive woody plants could have deleterious effects on animal nutrition, due to the deleterious effect of plant secondary compounds.</li> <li>2. The foliage of invasive woody species can provide nutrients, mainly protein, and could improve the ruminal environment.</li> <li>3. It is possible to find more forage species under canopy of some invasive woody species than in open areas (e.g., <i>Prosopis leavigata</i>, <i>Dichrostachys cinerea</i>).</li> <li>4. Canopy cover can significantly reduce the grass biomass depending on the density of the invader (e.g., <i>Dichrostachys cinerea</i>, <i>Terminalia sericea</i>, <i>Leucaena leucocephala</i>, <i>Prosopis juliflora</i>, <i>Acacia saligna</i>, <i>Hakea sericea</i>).</li> </ol>	<ol style="list-style-type: none"> <li>1. Aro et al. (2009); De Angelis et al. (2021)</li> <li>2. Ferrer et al. (2021)</li> <li>3. Hölscher et al. (2005); Ancira et al. (2006); Utaile et al. (2021)</li> <li>4. van Wilgen and Richardson (1985); Mandle et al. (2011); Randle et al. (2018)</li> </ol>



### 6.3 Management strategies for invasion control and their impact on general soil quality

Management of an invasion of a woody species is not limited to controlling the invading population but also addressing, as far as possible, the impacts of the invasion. This management is usually determined by the characteristics of the site, the species present, the size of the invasion, and the resources available to implement a control plan. To achieve more resilient ecosystems, the choice of how to manage invasive species must also maintain harmony with the benefits that these species have provided to the soil.

It has been shown that, depending on the type of management strategy used to control invasive woody species, the impact on soil can be dramatic. For instance, use of bulldozers or excavators with mulching devices or the use of herbicides applied directly to the soil disturbs the treated area, altering its physical and chemical characteristics (Campbell et al. 2019; O'Brien et al. 2022). Other strategies are more polemics regarding its impacts. For example, girdling stops the flow of carbohydrates below the soil, which would reduce substrate supply for microbes, constraining soil CO<sub>2</sub> flux, while maintaining soil temperature and moisture (Binkley et al. 2006; Liu et al. 2012). On the other hand, prescribed fires affect soil properties, especially soil's physical and biological properties but its impact differ greatly depending on soil initial characteristics, vegetation, or type of fire (Alcañiz et al. 2018; Daryanto et al. 2019).

In the search for better alternatives and considering the disruptive nature and negative impacts on the soil of conventional control methods, more ecological management strategies have been developed. For example, the use of grazing animals with browsing habits for the control of invasive woody shrubs has become a common practice for many low-income farmers, allowing them to contain the invasion in a relatively short time (depending on the stocking rate in the invaded area), while providing livestock with an alternative source of animal feed when pasture is not very productive or of poor quality. The impact of this practice on soil has been variable. For example, Lu et al. (2015) showed that there were no significant differences in soil bulk density, pH, particle size distribution, and aggregate distribution between free grazing and grazing exclusion. However, Futa et al. (2017) reported that soil pH, mineral nitrogen content, available phosphorus, and activity of dehydrogenases, phosphatases, and ureases enzymes were significantly higher in soils with free grazing compared to an ungrazed reference pasture. Another recognized control strategy is the planting of native species at highly degraded sites with dense invasion. This management involves cutting the invasive plants

(e.g., with machetes and mattocks) prior to planting (Raman et al. 2009).

As a final discussion, we have identified some points of controversy and gaps in knowledge (Table 7). The references that appear to exemplify each controversy do not necessarily represent the number of articles on this in the web of science, but rather are the examples cited in this article. Some of these controversies arise from the different impacts of these species on the ecosystem, either during the invasion or after their elimination.

## 7 Conclusion

It is increasingly realized that invasive woody species can be used in ecosystem restoration and to restore productivity of degraded agricultural land. The potential benefits and harms of these species are highly dependent on the interaction of the species with their immediate environment (climate, soil, vegetation, and animals), and on the socioeconomic context of the region. For instance, not all exotic species spread through disturbed areas, rather there are some species that can spread through native habitats where there is no local predator. In such case, we advocate measures targeted towards eradication or very strict containment/minimizing the population, while maintaining as much as possible the natural attributes of the colonized ecosystem (e.g., native vegetation, macro- and microfauna, water resources), which may be achieved (e.g., by girdling). However, if the reason for invasion is the fact that the ecosystem was completely disturbed, then maximum but wise management of the invasive species would be the choice to be made, because this can lead to ecosystem restoration. This may be achieved by browsing of woody plants (which in time may even lead to natural suppression of the invasive species). This approach provides the basis for talking about “pioneer plants” rather than “beneficial invasive plants,” emphasizing that the ecosystem that has evolved/the “new” ecosystem will not necessarily be a “better” ecosystem from a human perspective.

On the other hand, it is likely that the spread of exotic woody plants will continue to increase, no longer because of intentional or accidental introduction of the species, but as a consequence of increasing multiple anthropogenic pressures and the impact of climate change on ecosystems. Therefore, there will undoubtedly be an increasing need for disturbance-based management in the coming years, which will not be a one solution fits all, but rather will have to be context specific and tailored to the impacts posed by the invasive species.

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## Declarations

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