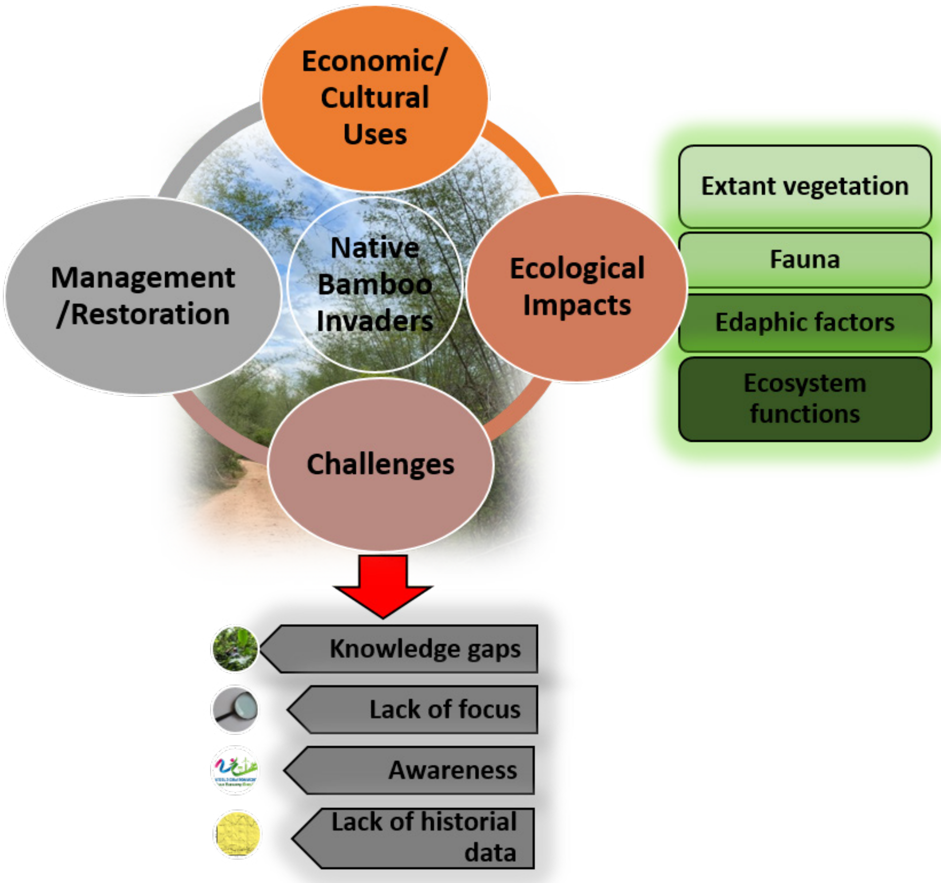
REVIEW ARTICLE

Native bamboos with invasive traits: impacts, consequences and challenges with special emphasis on Asia Pacific region

S. Madawala* and T. Wijewickrama



Highlights

- Invasive behaviour of 'native' species has often been overlooked until recently.
- Native invaders escape due attention owing to their many commercial uses.
- Some bamboo species expand their territories in native ranges in a rather ad hoc manner.
- Poor knowledge on 'native invaders' constraints feasible solutions for their control.
- This review highlights potential impacts, knowledge gaps and challenges.

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REVIEW ARTICLE

Native bamboos with invasive traits: impacts, consequences and challenges with special emphasis on Asia Pacific Region

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Abstract: Defying all norms of biological invasions, some native species expand their populations similar to their exotic counterparts causing potentially harmful impacts in native habitats. Despite an early caution by ecologists, they are now recognized as 'native invaders'. Though 'native' invaders may also incur harmful impacts similar to their 'exotic' counterparts, there are clear contrasts between them, thus demanding further studies to explore their life traits and cues that trigger their invasive traits. Among native invaders, bamboos are in the forefront due to their robust growth and resilience to harsh conditions. Also, it is a known fact that bamboo-dominated forests are on the increase globally while native forest are declining at a rapid rate. This review attempts to condense the current understanding of 'native' bamboos that spread in the Asia Pacific region with invasive potential and their short- and long-term ecological impacts. Possible environmental cues that may trigger their 'invasive' nature are also discussed. Of many, climate change seems to be the major driving force triggering their invasive behavior, though long-term studies are needed to ratify this link. Major challenges and knowledge gaps that hamper their control have also been deliberated. The evidence confirmed that native bamboos have the potential to incur negative impacts on ecology, social and economic aspects. However, their impacts are not always in parallel with that of 'exotic' invaders, thus cautioning any attempt of generalization. The lack of comprehensive research and historical information are considered as major impediments to identify suitable measures to manage them effectively. Further studies are mandatory to fill the existing knowledge gaps and to identify challenges to bring about effective management strategies to control 'native' bamboos with invasive potential.

***Keywords*:** Bamboos; native invaders; ecological impacts; population expansions; native ranges; challenges.

INTRODUCTION

Until recently, studies have been carried out to recognize local, regional, and global driving forces accountable for the decline of native populations (Parmesan, 2006). Among other causes (*i.e.* land degradation, habitat loss, fragmentation and climate change), exotic invasive species are identified as one of the major contributors for the decline and extinction of native species (Harrison *et al*., 2006). Later, the ability of some native species to expand their territories similar to 'exotic' invaders has been emphasized. They expand populations into nearby natural and man-made habitats, sustaining potentially detrimental impacts (Campanello *et al*., 2007; Larpkern *et al*., 2011; Carey *et al*., 2012; Bai *et al*., 2013). However, the ability of native species to invade their home ranges and beyond did not receive the due recognition soon possibly due to the subtle nature of this emerging issue (Carey *et al*., 2012; Valéry *et al*., 2013). Garrott *et al*. (1993) rightly raised the importance of this evolving issue of 'native' invaders for the first time, with gaining momentum in research a decade later (Table 1). The baseline information on 'native' invaders could be crucial for policy makers to take tangible decisions in managing threatened habitats in an effective manner.

Among the known 'native' invaders, bamboos are in the forefront due to their exclusive life traits including fast growth, clonal reproduction, high phenotypic plasticity and competitive ability. It is reasonable to speculate that the sudden population expansion of bamboos may also incur similar or even harsher consequences to that of 'exotic' bamboo species. Thus, the present review attempt to critically analyze the recent literature on 'native' bamboos to describe ecological impacts following sudden population expansions. In addition to revisiting the available literature to evaluate impacts, the knowledge gaps and potential challenges were identified and discussed. The need for more focus on the 'invasive' behavior of native species under different habitat-climate settings to make informed predictions of their further expansion has also been highlighted (Carey *et al*., 2012; Dida *et al*., 2021).

Bamboos (Family: Poaceae) attract a global interest due to its uncommon life cycle, ecological significance, and a variety of commercial and cultural uses. Bamboos come from a single subfamily, Bambusoideae (Kigomo, 1988) which divides into three tribes, Olyreae (herbaceous), Bambuseae (tropical woody) and Arundinariaeae (temperate woody) (Ramanayake *et al.,* 2007; Kelchner and BPG, 2013). Unlike other plant groups, the classification of bamboos sets challenges mainly due to paucity of reproductive structures. In 1988, Rao *et al*. noted 1,250 species of bamboo under 74 genera. Later on,

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Table 1: A list of literature published globally on native bamboo invaders during the past decade.

Bamboo species	Focus of the study	Forest type/Country	Reference
Guadua tagoara	Seedling community	Brazilian Atlantic Forest	Rother *et al*., 2018
Guadua tagoara	Seed rain and seed limitation	Brazilian Atlantic Forest	Rother *et al*., 2009
G. weberbaueri	Seed rain	Terra-firme forests in the Amazon, Brazil	Bona *et al*., 2020
Phyllostachys edulis	Soil microbial community	Subtropical forests in southern China	Tian *et al*., 2020
Chusquea ramosissima *C. tenella*	Impacts on tree saplings	Semi-deciduous Atlantic Forest, Argentina	Montii *et al*., 2013
Guadua sarcocarpa	Life traits and phenology of bamboo	Upland forests of the southwest Amazon	Carvalho *et al*., 2013
Phyllostachys pubescens	Soil organic carbon and arbuscular mycorrhizae	Mixed coniferous and broadleaved forest in the northern subtropics of China	Qin *et al*., 2017
Guadua sarcocarpa *G. weberbaueri*	Management of bamboo-dominated forests through logging	Southwestern Amazonia	Rockwell *et al*., 2014
Phyllostachys pubescens	Net Primary Productivity and N cycling	Evergreen broadleaved forest in subtropical China	Song *et al*., 2017
Phyllostachys edulis	Structure and diversity of soil microbial community	Subtropical monsoon forest in southeastern China	Xu *et al*., 2015
Phyllostachys edulis	Soil C and N pools	A nature reserve in southeastern China	Bai *et al*., 2016a
Guadua sarcocarpa *G. weberbaueri*	Physical damages on tree recruitment	Terra firme tropical moist Amazonian forests in south-eastern Peru	Griscom and Ashton, 2006
Guadua tagoara	Forest structure and dynamics	Atlantic Forest of southern São Paulo State, Brazil	Lima *et al*., 2012
Moso bamboo	Human disturbances as a contributory factor for invasion	Broadleaved forest in southern China	Bai *et al*., 2016b
Bambusa tulda *Cephalostachyum pergracile*	Tree regeneration	Tropical monsoon forest in Thailand	Larpkern and Totland, 2011
Bambusa tulda *Cephalostachyum pergracile*	Tree regeneration	Mixed deciduous forest in northeastern Thailand	Larpkern *et al*., 2011
Phyllostachys edulis	Species diversity and dynamics	A nature reserve in China	Bai *et al*., 2013
Chusquea valdiviensis	Bird population	Temperate forest in southern Chile	Reid *et al*., 2004
Guadua sarcocarpa	Fire as a factor contributing for bamboo expansion	Guadua-dominated forests of the south-west Amazon	Smith and Nelson, 2011
Guadua tagoara	Avian assemblages	Brazilian Atlantic forest	Rother *et al*., 2013
Phyllostachys edulis	Soil biochemical properties	Japanese cedar (Cryptomeria japonica) forest	Shiau and Chiu, 2017
Sasa chartacea	Understory plant community	Plains in Japan	Tomimatsu *et al*., 2011
Guadua tagoara	Phylogenetic structure of seeds and seedling community	Old-growth Atlantic Forest	Schweizer *et al*., 2017
Sasa palmata *S. kurilensis*	Tree regeneration	Beech forest in Japan	Masaki *et al*., 2021
Phyllostachys heterocycla	Soil bacterial community structure	Broadleaved forest in southern China	Zhang *et al*., 2020
Woody bamboos	Tree density and basal area	Andean Forests	Fadrique *et al*., 2021
Guadua weberbaueri	Litter dynamics	Amazonian forest, Brazil	Dantas *et al*., 2020
Not specified	Drought mediated fires as a factor for expansion	Amazonian forest, Brazil	Da Silva *et al*., 2021
Aulonemia aristulata	Seed rain	Tropical temperate forest in southeastern Brazil	Grombone-Guaratini *et al*., 2014

Phyllostachys edulis	Precipitation as a factor for bamboo distribution	China	Shi *et al*., 2020
Guadua spp.	Community structure of beetles	Terra firme forests in Peru	Jacobs *et al*., 2018
Bambusa bambos	Abundance and richness of AMF	Tropical Moist Evergreen Forests, Sri Lanka	Mafaziya *et al*., 2019
B. bambos	Community perceptions on bamboo spread	Tropical Moist Evergreen Forests, Sri Lanka	Wijewickrama *et al*., 2019
B. bambos	Structure and composition of the extant forest community	Tropical Moist Evergreen Forests, Sri Lanka	Wijewickrama *et al*., 2020
B. bambos	Seedling recruitment, mortality and regeneration potential	Tropical Moist Evergreen Forests, Sri Lanka	Wijewickrama *et al*., 2021 (in press)
B. bambos	Litter-dwelling arthropod community	Tropical Moist Evergreen Forests, Sri Lanka	Wijewickrama *et al*., (unpublished)

Figure 1: *Ochlandra stridula*, an endemic bamboo species in Sri Lanka and in the Western Ghats in India, showing a tendency to expand its populations in forests in the lowland wet zone of Sri Lanka. © Tharanga Wijewickrama.

1,662 species of bamboos were identified in 121 genera (Canavan *et al*., 2016), adding a significant number to the list. Based on molecular studies, the tribe Bambuseae was further divided into 11 subtribes; whereas Olyreae into 3 subtribes (Kelchner and BPG, 2013; Soreng *et al*., 2017). The subtribal classification of Bambuseae and Olyreae seems clearer than that of Arundinarieae (Zhang *et al*., 2021). The most recent literature observed nearly 1,700 bamboo species in 127 genera (Clark and Oliveira, 2018).

Over the years, bamboos are introduced intentionally outside their native ranges for numerous purposes, and over time some become invasive causing harmful impacts on biodiversity and ecosystem services (Fukushima *et al*., 2015; Umemura and Takenaka, 2015). Of all bamboo species, a few are categorized as 'exotic' invaders, of which the majority are 'running' bamboo species. The 'native' bamboos are considered as an important component in forest ecosystems, until a few turn into 'invasive' triggered by unknown environmental cues. *Phyllostachys edulis* (*moso* bamboos) and *P. bambusoides* in China and Japan (Yang *et al*., 2008; Bai *et al*., 2013; Xu *et al*., 2015), few species belonging to *Chusquea* and *Guadua* genera in Atlantic forests in the South America (Montii *et al*., 2011; Lima *et al*., 2012; Rother *et al*., 2016), *Bambusa bambos* in south-east Asia (Canavan *et al*., 2016; Jayawickrama *et al*., 2019, 2020) and *Ochlandra stridula* (an endemic) in Sri Lanka [(Prematilleke *et al*., 2014) (Figure 1)] are some known 'native' bamboo species with an invasive potential. Unfortunately, 'native invaders' evade attention from the conservationists due to the general assumption that all native species are harmless. Pivello *et al*. (2018) named 'native' invaders as 'super-dominant' natives and identified 16 such terrestrial species that need attention in Brazil, out of which 5 belonged to bamboos.

Limits of the review

Though both 'native' and 'exotic' bamboos are known for their 'invasive' behaviour (Bai *et al*., 2013), this review will focus only on 'native' bamboo species displaying 'invasive' potential. Despite receiving less attention on their adverse impacts, few studies have been carried out in the Asia-Pacific region exploring ecological impacts of native bamboo invaders, revealing a new *vista* for further research. Despite the growing interest on this emerging issue, the information on short- and long-term ecological impacts of native bamboos is still scanty and unambiguous. Thus, the main objective of this review is to examine the available scientific literature on 'invasive' native bamboo species and their potential impacts to shed light on the severity of this long-ignored issue, and to ascertain underlying causes for their unusual behavior. In order to impose a self-boundary, the review focuses mainly on related literature from the Asia-Pacific region. This review may also attempt to identify knowledge gaps that need further investigation, challenges that impair the policy makers, and finally to make recommendations to control further invasion and mitigate their potentially detrimental impacts.

Invasion *versus* over-dominance

Invasion of exotic/alien species and their impacts are well-documented globally. Of many definitions of 'invasive species', the common fact is that the focal species should be an 'alien'/ 'exotic' or a 'non-native'. This is the major reason for discounting 'native' invaders by conservationists and scientists. With the steady growth of publications highlighting the enormity of this evolving problem, a new definition is introduced to overcome this disparity. In place of 'invasion', the terms 'over-abundance' (or 'over-dominance') and 'expansion' have been proposed to evade unnecessary overlaps (Conlisk *et al.,* 2013; Wijesundara, 2017), while Simberloff (2012) termed this special group of 'native' plants as 'native' invaders.

While impacts of 'exotic' invasive species are relatively well-explored under diverse climate and habitat conditions, the impacts of 'native' invaders are less known (Lima *et al*., 2012). It is quite justifiable to foresee that the impacts of 'native invaders' are more or less comparable to that of 'exotic' invaders. However, the dearth of studies on 'native invaders' make it difficult to contrast and generalize impacts under different habitat-climate settings. Thus, this review would pave the way to find likely similarities and/or dissimilarities between these two groups of plants and their so-called more or less similar circumstances, 'invasion' and 'expansion', with the available literature.

Bamboo: it's current distribution

Multiple economic uses together with intrinsic life traits give bamboos a distinctive place amongst other terrestrial plants. Bamboos are rapid-growing plants with unusual flowering patterns. Ghinkul (1936) classified bamboos into three groups based on their senescence behavior, though a majority are known to possess a single reproductive event in its life cycle which involves massive flowering followed by mass death [(Keeley and Bond, 1999), Figure 2].

Over 6.3 million km^2 of bamboo forests are reported to exist from Northeastern India through Burma to Southern China, and also from Sumatra to Boneo (Bystriakova *et al*., 2003). Bamboos show the highest species richness in the Asia-Pacific region, followed by South America and Africa (Bystriakova *et al*., 2003). In the Asia-Pacific region, China has recorded the highest species richness (626 species), followed by India with 148 species (Sharma and Nirmala, 2015). The highest species richness per area (with 144 species per km^2) is also recorded in forests in Southern China. In India, more than 50% of the naturally occurring bamboo species are known to be endemic. *Bambusa, Dendrocalamus* and *Ochlandra* are the three most dominant genera in India with each representing more than 10 species, which represent 45% of the total bamboo species in the country (Sharma and Nirmala, 2015). In the South American sub-continent, Brazil has the greatest bamboo diversity (137 species). The clump-forming bamboos are rich in the tropical belt (Uchimura, 1987), while the herbaceous bamboos are confined mainly in the Neotropics of Brazil, Paraguay, Mexico and West Indies (Yeasmin *et al*., 2015).

Despite bamboos growing naturally in all major continents except in Europe (with the ability to thrive from just above sea level to 4,000 m), their distribution is known to be highly irregular (Behari, 2006; Goyal *et al*., 2012). Globally, woody bamboos are distributed in three major regions *viz.,* paleotropical (tropical and subtropical regions of Africa, Madagascar, Sri Lanka, India, Southern Japan, Southern China and Oceania), neotropical (Southern Mexico, Argentina, Chile and West Indies), and North temperate (North Temperate Zone and at higher elevations of Madagascar, Africa, India and Sri Lanka). In the tropics

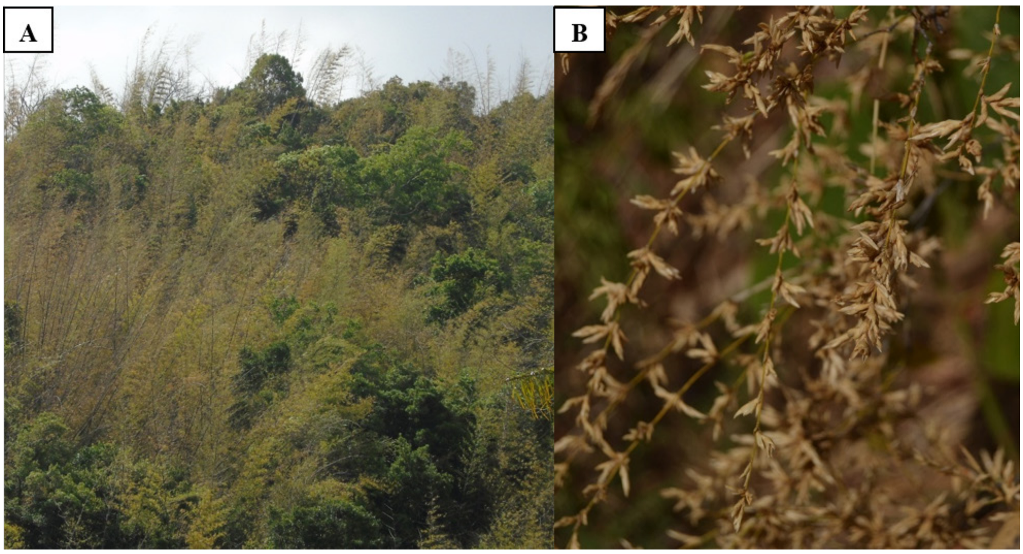

Figure 2: Bamboos play an important component in both wet and dry zone forests in Sri Lanka. A: the spread of native *Bambusa bambos* in moist evergreen forests in Sri Lanka altering the forest structure and composition; B: flowering of *B. bambos*. Location: Moragahakanda, Naula, Sri Lanka © Imesh Weerasinghe and Tharanga Wijewickrama.

and sub-tropics, bamboos forests encompass a total extent of 22 million hectares (Zhou *et al*., 2005). While broadleaved forest cover is dwindling rapidly, the extent of bamboo forests has been gradually expanding over time (Zhou *et al*., 2005). China, in particular, has increased its bamboo forest cover steadily to an extent of 5 million hm^2 as at 2000 (Xiao, 2000).

Though bamboo is considered as a major component in tropical forests, some countries, such as Sri Lanka, do not identify bamboo forests in its major forest classifications due to its rather localized distribution. According to Soderstrom and Ellis (1988), Sri Lanka has three subtribes of Bambuseae, which include six genera and 12 species. In the subtribe of Arundinariinae, there are five species of genus *Arundinaria*. The subtribe Bambusinae comprises three genera, *Bambusa, Dendrocalamus* and *Pesudoxytenanthera,* while the subtribe Schizostachydinae is represented by *Ochlandra stridula* and *Davidsea attenuata*.

Uses of bamboo

Bamboos provide many important ecosystem and economic services to their native and introduced ranges. In terms of ecological impacts, bamboos facilitate forest dynamics through distinct flowering events and die offs (Keeley and Bond, 1999). Bamboo plays a critical role in carbon storage, water and soil conservation, and even in mitigating impacts of climate change (Zhou *et al*., 2005; Song *et al*., 2015) (Figure 3). Bamboo forests tend to retain soil moisture through increased litter production and accumulation (Shinohara *et al*., 2015). High biomass production may also contribute positively to the rehabilitation of degraded lands. Bamboos are also use in agroforestry systems in China, India and Thailand (Fu *et al*., 2000). Bamboo forests are known as efficient carbon sinks (Zhou and Jiang, 2004; Song *et al*., 2015), with exciting numbers to back their contribution in the climate change mitigation. In China, the carbon density in bamboo forests ranged from 168.7 to 259.1 t C ha^{-1} which is much higher than that of many other forest types (38.7 t C ha^{-1}) as well as the global average of 86 t C ha^{-1} (Lou *et al.*, 2010).

In addition, there are many known intriguing relationships of bamboos with animals indicating their long history in the evolutionary trajectory. Some animals prefer bamboo-dominated forests over other forest types (Rockwell *et al*., 2014), especially during mast fruiting episodes (Sieving *et al*., 2000), probably due to the bounteous availability of food. Reid *et al*. (2004) showed compelling evidence to suggest that some bird species prefer the undergrowth of bamboo-dominated forests over others without bamboo. However, Coggins (2000) categorized bamboo plantations in South-East of China as the least valuable habitats for wildlife, indicating species-specific preferences by animals.

In addition to crucial ecological services, bamboos have many other commercial, agricultural and cultural uses as well. Bamboos show a high potential as a commercial commodity due to their rapid growth with zero inputs. Thus, it is one of the most significant non-timber forest products (NTFP) in the Asia-Pacific region. Being termed as ‘poor man’s timber’, the rural people opt bamboo as a raw material in construction, agriculture and farming activities for decades. However, the commercial value of bamboos has diminished gradually over the years, with a renewed interest in recent times. Bamboos are used for many diverse and innovative practices in cottage-based industries and in poverty alleviation programs. In India, thorny bamboo species have been explored as a potential alternative for electric fencing to ward off wild elephants from human settlements and tea plantations (Dutta, 2016). However, this has been disputed by a recent study carried out in Sri Lanka where local communities claimed an intensified presence of elephants since the expansion of thorny *B. bambos* perhaps due to high palatability of young bamboo shoots (Wijewickrama *et al*., 2019). However, in recent times, bamboo has been identified as a source of sustainable raw material to reduce the demand on other timber sources.

Figure 3: *Dendrocalamus* sp. are often discovered close to streams. Location: Doi Hang, Chiang Rai, Thailand. © Binu Samarakoon, Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai, Thailand.

Figure 4: *Moso* bamboo (*Phyllostachys* sp.) groves at Moganshan, Hangzhou, Zhejiang Province, China. © Charlotte King, International Bamboo and Rattan Organization (INBAR).

Invasive nature of bamboos

Bamboos in general are less likely to invade habitats due to their rare flowering events and their preference for narrow range of environmental conditions to thrive. For a long time, conservationists were reluctant to recognize them as 'invasive' possibly owing to their known economic and cultural uses. As a result, they rarely appeared in 'potential-for-expanded-distribution lists in country reports. As of 2016, only 12 woody bamboo species (0.7%) had been formally identified as 'invasive' (Canavan *et al*., 2016). Relatively more literature is available on invasiveness of exotic bamboo species and their impacts on biodiversity, ecosystem, and their services (Pagad, 2016). In contrary, the 'invasive' nature of native bamboo species received due attention much later.

While natural forest cover is in the decline world over, bamboo forests are expanding their territories in a rather unprecedented manner, especially during the last few decades. In China, the area under bamboo has increased by 14.5% during a span of 9 years since 2004, which is nearly 10% higher compared to the previous decade (Xu *et al*., 2020). The area under the native *moso* bamboo has been extended markedly over the years [(Chang and Chiu, 2015; Bai *et al*., 2016), Figure 4]. In Japan, a massive increase (270%) of bamboo forests from year 1961 to 1978 was recorded (Okutomi *et al*., 1996), with similar increases reported in Brazil and India (Kudo *et al*., 2011; Lima *et al*., 2012; Dutta and Reddy, 2016; Kudo *et al*., 2018). In a survey carried out using satellite images from 1973 to 2012, nearly 21% of evergreen forests in Western Ghats has shown to be invaded by a native reed bamboo, *Ochlandra travancorica* (Dutta and Reddy, 2016). A similar development was also reported in India with another native bamboo species, *Yushania maling* (Roy *et al*., 2016; Srivastava *et al*., 2018). These long-standing figures clearly highlight the ability of some bamboo species to expand their territories irrespective of their ecological status.

It seems that both exotic and native bamboos contain similar plant attributes to facilitate their 'invasive' behavior *viz.,* rapid growth, clonal reproduction, phenotypic plasticity, competition and allelopathy (Yang *et al*., 2015). Despite their rare flowering events and subsequent seed production, the ability of bamboos to reproduce through clonal stems together with their inherent rapid growth have transformed them into aggressive invaders. With flowering cycles far apart, bamboos mainly spread through clonal growth (Xu *et al*., 2020). In addition to their inherent attributes, bamboos also take advantage over other co-occurring species by making their immediate environment inhospitable for others to sustain. With long culm lengths and high crown position, bamboo species, such as *P. pubescence*, are able to penetrate the canopy of broadleaved forests casting a significant shade over the forest floor, transforming the forest undergrowth unfavorable for emerging seedlings and their survival (Isagi and Torii, 1997). Studies also observed that some bamboo species thrive in clay-rich soils while others prefer rocky slopes with southerly, southeasterly or easterly aspects (Lima *et al*., 2012; Ying *et al*., 2016; Wijewickrama *et al*., 2019). The extant vegetation and land use, and spatial and topographic features are identified as main contributory factors for *P. pubescens* invasion (Suzuki, 2015), suggesting the importance of both intrinsic and extrinsic factors that may facilitate their population expansion.

The ability of plants to adjust to suit changing conditions (*i.e.* plasticity) is a crucial attribute in exotic species to determine their invasive success (Hodge, 2014). Bamboos too have shown their ability to adjust to moving conditions (Montti *et al*., 2014; Winkler *et al*., 2016). Some woody bamboo species show high plasticity in terms of structural and functional leaf traits in response to different light conditions (Montti *et al*., 2014), while others showed a greater plasticity in response to physical and physiological stress (Lima *et al*., 2012). High plastic nature seems to play a crucial role in determining the invasive potential of 'native' bamboos as well. However, the dearth of studies on bamboos and their potential eco-physiological traits under varying environmental conditions can be highlighted as a drawback in concluding and predicting their invasive behavior despite their 'native' status.

External factors responsible for sudden expansion of bamboo

Human-induced environmental changes are known to modify vegetation dynamics (Franklin *et al*., 2016). Available research is mostly focused on gradual decline of plant populations or extinctions triggered by environmental changes (Chang *et al*., 2015), while overlooking population expansions. Both anthropogenic and/or natural disturbances are identified as main drivers accountable for range and compositional shifts in plant communities, in which the 'less tolerable' species (or 'losers') tend to decline and are replaced by 'more tolerable' species ('winners') (McKinney and Lockwood, 1999). Exotic species are considered as 'winners', while the 'natives' often go unnoticed (Mack *et al*., 2000; Stohlgren *et al*., 2008). While species invasion and habitat modifications are identified as major causes for the decline of native species (Didham *et al*., 2007), much studies have not been done to ascertain the actual causes of their rapid expansion in home ranges. Regular and mild anthropogenic disturbances are known to play a crucial role in shaping the structure and composition in communities (Sheil, 2016), but when they exceed a certain threshold level (in terms of magnitude, timing, and variability), they seem to trigger a population expansion of some native species (Catford *et al*., 2012; Pivello *et al*., 2018). Accordingly, some speculate that anthropogenic and natural disturbances and their interactions may also assist sudden population expansion of bamboos, though their precise underlying mechanisms are not yet fully understood (Bai *et al*., 2013).

The climate change is identified as one of the causes of modifying plant populations and communities (Chang *et al*., 2015). In favour, phenological and range shifts in plants (and animals) are observed in parallel with the anthropogenic global warming (Parmesan and Yohe, 2003; Lenoir and Svenning, 2015). Climate change influences plant species differently (Lewis *et al*., 2004; Zuidema *et al*., 2013), where highly abundant species are prone to decrease their population growth rates (Chang *et al*., 2015), while highly localized populations, such as native bamboos, tend to expand. However, there is no solid evidence to support that range shifts of some species are solely driven by temperature-induced causes, such as dispersal behavior, mortality and survival (Parmesan and Yohe, 2003; Parmesan, 2006). Considering all these facts, it can be hypothesized, that once the dominant species in forest communities decline or shift their ranges due to climate change or its related factors, other opportunistic species such as bamboo with high tolerance to extreme climatic conditions and rapid growth take advantage of the situation, thus expanding their populations in an unprecedented manner.

Human activities are also known to trigger native species to expand populations in home ranges (Carey *et al*., 2012). These population growths sometimes may go unchecked causing alterations in dominance hierarchies in plant communities (Goodrich and Buskirk, 1995; Valery *et al*., 2008). Thus, human-mediated habitat changes may drive individual effect of native species (both plants and animals) on its resident community, increasing the levels of predation and competition. Such situations may facilitate the native species to become dominant in the community by exploiting and filling vacant niches that left behind by other native species (Didham *et al*., 2007). The changes to dominance hierarchies of plant/animal communities cause substantial modifications to the biotic component and its interactions, if the new dominant species is drastically differed from the former (Larpkern *et al*., 2011). This could be another possible scenario of how some native bamboo species are becoming dominant in their home ranges.

A study carried out in a mixed deciduous forest in Northeastern Thailand suggests that human-induced disturbances be responsible behind expansion of *Bambusa tulda* and *Cephalostachyum pergracile* populations, causing significant changes to the extant woody vegetation. Though some support the notion that human-mediated disturbances cause bamboos to expand (Tripathi *et al*., 2006; Yang *et al*., 2015), others do not. A study carried out in China reported a population expansion of a native *moso*

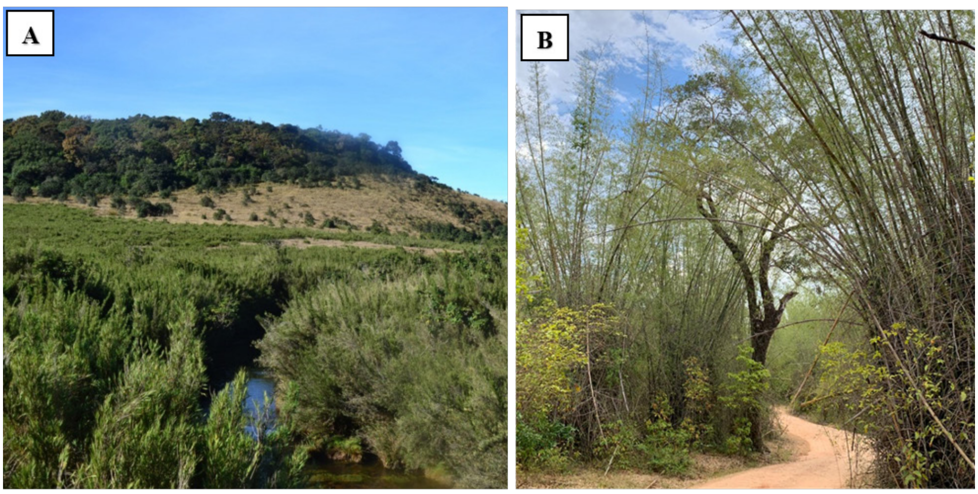

Figure 5: A: *Kuruna densifolia* (an endemic), B: *Bambusa bambos* (a native) are expanding their populations in the Horton Plains National Park in the Central Highlands and Minneriya National Park, North Central Province of Sri Lanka, respectively. © Tharanga Wijewickrama and Imesh Weerasinghe.

bamboo species with no apparent human interventions, suggesting the complexity of the present understanding of native invaders (Bai *et al*., 2016).

Despite some positive relationships of human-induced drivers and species declines/extinctions and/or shift ranges (Franklin *et al*., 2016), concrete evidence to support this theory is still scarce. Few studies speculate a connection between human-induced drivers and sudden expansion of plant populations, and even identify climate change as the most significant causal factor (Fernandez-Going *et al*., 2012; Conlisk *et al*., 2013; Vanderwel and Purves, 2014). However, it is right to suggest that bamboos are particularly more vulnerable to climate change due to their lack of ability to adapt as a result of unusually lengthy flowering cycles and rather limited seed dispersal ability (Taylor *et al*., 1991). In favour, a study carried out in China observed a climate-driven reduction of three bamboo species causing adverse consequences on the panda population (Tuanmu *et al*., 2013). *Kuruna densifolia* (an endemic) and *B. bambos* (a native) are expanding their populations in highly protected areas in Sri Lanka, further supporting the pivotal role played by the climate change for their invasive behaviour where human disturbances are minimal (Figure 5).

In addition to human-mediated causes, other factors are also debated in order to explain sudden expansion of bamboo populations. Bamboos produce nutritious seeds with no known toxicities, hence making them a good food source for animals (Chatterji, 1960). During masting events, the seed predators of bamboos thrive, expanding their populations and at the same time aiding the expansion of bamboos. In addition, massive seed production and rapid growth, the absence of large mammals predate on bamboo seeds, seedlings, and their young shoots may also indirectly help bamboos to expand their populations (Galetti *et al*., 2009). Fire is another driving force that seems to assist the expansion of bamboo into neighboring areas. A study carried out in *Guadua sarcocarpa* dominated forests in the South-West Amazon concludes that forest fires could expedite the bamboo spread (Smith and Nelson, 2010). In favour, da Silva *et al*. (2021) also concludes that drought-induced forest fires can shift these tropical lowland forests towards bamboo-dominated forests, with the caution of the possibility of this becoming even worse with more frequent fires owing to global warming.

Suzuki (2015) justly highlights the complex nature of this issue by emphasizing the interactive nature of biotic and abiotic factors that may facilitate the expansion of bamboo. Ying *et al*. (2016) noted that evergreen broadleaf forests are more prone to *moso* bamboo (*P. pubescencs*) invasion than deciduous broadleaf and coniferous forests, suggesting their preference for specific edaphic and micro-climatic conditions to further expand. The plastic nature of bamboos (both morphological and physiological) to environmental parameters such as soil moisture (*i.e.* a dwarf bamboo, *Sasa kurilensis*), could also play a pivotal role in their rapid expansion (Winkler *et al*., 2016). Some bamboo species (*i.e. Guadua tagosra* and *Bambusa bambos*) seem to prefer clay-rich soils for their establishment (Lima *et al*., 2012; Wijewickrama *et al*., 2020), while major flood events coincide with mast seeding may also contribute to population expansion of bamboo species, *Merostachys riedeliana* (Oliveira-Filho *et al*., 1994). The succeeding micro-climate changes driven by forest fragmentation (such as light and soil moisture) have been identified as probable facilitators for range expansion of a dwarf bamboo species, *Sasha chartacea* (Tomimatsu *et al*., 2011). Allelopathy is known to aid plants to expand territories in both native and introduced ranges. A native bamboo species, *Merostachys riedeliana* that overabundant in Brazilian Atlantic Forests, has shown high to moderate allelopathic activity, thus earmarking as one of the major underlying causes for its superior ability to expand (Jose *et al*., 2016). The overall evidence displays the complexity of underlying mechanisms contributing to population expansion of native bamboo invaders.

Bamboo driven ecological impacts

From time to time, scientists have justly pointed out the importance of deliberating on 'native invaders' and their potential impacts on home ranges (Carey *et al*., 2012; Yang *et al*., 2015; Pivello *et al*., 2018). It is valid to suggest that when native species expand their populations in home ranges, they consume the available resources at the expense of other co-occurring species, thus causing them to decline (Arim *et al*., 2006). Such 'super-dominant' species may influence not only the structure and composition of its resident community, but also some vital functions, such as pollination, seed dispersion and nutrient cycling, thus converting the ecosystem into a new realm. These changes together with subsequent micro-climatic modifications influence the natural regeneration of the community causing long-term irreversible changes (Simberloff *et al*., 2012). Therefore, it is vital to detect these 'native invaders' in their early stages and their potential influences in order to introduce strategies to overcome any detrimental changes in their home ranges.

Despite some evidences to support that over-dominance of bamboos influence crucial community parameters and processes, information on short- and long-term impacts in different habitat-climate settings is relatively scarce due to lack of attention on 'native' invaders. In the recent past, studies have been carried out in countries, such as China, Japan and Brazil, exploring possible impacts of over-dominance of bamboos, with more focus on extant vegetation and some edaphic properties. Ecosystem functions, such as nutrient cycling, seedling recruitment, regeneration potential and soil biology, have enticed relatively poor attention. Therefore, these crucial aspects need to be explored in order to determine overall effects of bamboo over-dominance on home ranges.

Vegetation characteristics

Biomass, density, and diversity

Whether it is a native or an exotic, single-species dominance could inflict modifications to its plant community by altering the structure, composition and diversity. The diffusing nature of woody bamboos and their mass flowering events alter the micro-environmental conditions in their invading habitats. These micro-environmental changes could eventually trigger long-term structural and compositional changes in forest communities (Budke *et al*., 2010). The rapid growth of bamboos and their high competition for resources may add new dimensions to this issue. Larpkern *et al*. (2011) observed a decrease in woody seedling abundance, richness and diversity in bamboo-dominated forests, highlighting it as a clear sign of altering the structure of the extant vegetation in time. Bai *et al.* (2013) also observed a negative effect on plant diversity as a result of *moso* bamboo invasion in a coniferous, broadleaved forest in China. Lima *et al*. (2012) noticed a lower density of mature trees and species richness in an Atlantic forest dominated by a native bamboo species, *Guadua tagoara*. Long-term study in Southern Brazil indicates a low species diversity that fluctuates greatly over time in comparison to bamboo-free *Araucaria* forests (Lacerda and Kellermann, 2019). A lower recruitment rates together with high mortality seem to be major contributory factors for lower abundance of mature trees in bamboo-dominated communities. In Brazil, the forest gaps created by dieback events of *Merostachys skvortzovii* have facilitated the reestablishment of light-loving bamboos, thus exerting a negative influence on the tree seedling emergence (Greig *et al*., 2018). Several other studies too observed a decline in diversity due to over-dominance of bamboos (Larpkern *et al*., 2011; Kudo *et al*., 2017). In contrast, an increase in plant diversity was observed in a study done in Sri Lanka (Wijewickrama *et al*., 2020), though the increase is due to the establishment of light-loving non-forest species facilitate by bamboo-driven micro-climatic modifications. However, the same study detected no marked difference in tree densities in native forest patches with and without *B. bambos*.

The above-ground biomass is another crucial indicator of ecosystem health in forests. Bamboo-dominated forests show lower plant biomass in comparison to non-bamboo forests (Griscom and Ashton, 2003; Lima *et al*., 2012), while others reveal a higher annual biomass in *moso* bamboo forests in comparison to subtropical forests in China (Zhou and Jiang, 2004). A significantly greater net primary productivity in bamboo-dominated forests in comparison to nearby secondary evergreen broadleaved forests was observed by other workers too (Xiao *et al*., 2007; Xie *et al*., 2014). These findings suggest that bamboo dominance impose contrasting effects on forest communities which mainly depend on differences in climate-habitat settings thereby discouraging any over-simplification of bamboo-driven impacts without considering other on-site characteristics.

Species composition

The over-dominance of bamboos alters the species composition in both natural and semi-natural forests (Tabarelli and Mantovani, 2000; Griscom and Ashton, 2003; Guilherme *et al*., 2004; Larpkern *et al*., 2011), encouraging structural modifications over time. The bamboo-driven structural changes in forest communities are generally triggered by changes to tree recruitment and tree mortality (Guilherme *et al*., 2004). Bamboos do not affect all forest species and their maturity stages alike (Lacerda and Kellermann, 2019; Fadrique *et al*., 2020). Tall canopy and pioneer trees are the least affected as they both have the ability to break free from the dominance caused by bamboos, while the understory trees suffer the worst. Canham and Marks (1985) observed that bamboos facilitate seedlings of certain species while discouraging others. Wijewickrama *et al.* (2020) also observed a similar selective effect where *B. bambos* dominance favours light-loving species while discouraging shade-loving forest species under its canopy. Such species-specific preferences, encouraged by micro-climatic modifications to the forest interior due to bamboo dominance, may eventually lead to alter the composition and structure of bamboo-rich forest communities over time (Okutomi *et al*., 1996; Gonzalea *et al*., 2002; Lima *et al*., 2012).

Tree mortality

The mortality incidences have been intensified globally over the past few decades lowering the quality of forest communities. The most frequently implicated factors for forest dieback are elevated temperature, drought/water stress and air pollution. In a local scale, high tree mortality incidences in forest communities have been associated with both natural and anthropogenic causes including altered microclimatic conditions, wind turbulence, lianas and bamboos (Laurance *et al*., 2000; Nascimento and Laurance, 2008; Medeiros *et al*., 2013). Recent studies highlight a close link between bamboo-dominance and tree mortality, where bamboos seem to inflict direct and/ or indirect impacts on trees leading to their early deaths [(Laurance *et al*., 2000; Ferreira *et al*., 2020; Wijewickrama *et al*., 2020; Fadrique *et al*., 2021), Figure 6]. Bamboos are known to inflict more damage on late successional species than pioneers (Swaine and Whitmore, 1988). Though the precise mechanism is still not known, different hypotheses are set forth to explain this disturbing phenomenon in bamboo-dominated forest communities. According to Ferriera *et al*. (2020), the regular die-offs in bamboo forests accumulate high fuel loads triggering forest fires during dry seasons killing canopy trees. This hypothesis has been favored by previous workers as well (Keeley and Bond, 1999; Veldman and Puts, 2011), suggesting forest fires as one of the major causal factors for high mortality in bamboo forests.

Though tree mortality and bamboo density are factors known to relate closely (Medeiros *et al*., 2013), the potential bamboo-driven effects and their underlying mechanisms may vary between ecosystems and species (Fadrique *et al*., 2021). According to literature, physical damages from falling bamboo culms, changing microclimate, selective regeneration, allelopathy and edaphic factors are also implicated as possible causal factors for tree deaths in bamboo forests (Griscom and Ashton, 2003; Campanello *et al*., 2007; Montii *et al*., 2011; Jose *et al*., 2016). Though lianas are an integral component in tropical forests, they are known as 'structural parasites' owing to their ability to compete for resources (Swaine and Grace, 2007; Schnitzer and Bongers, 2011). When the lianas

Figure 6: A spread of *Davidsea attenuate*, a native bamboo species, in lower montane forests in the Knuckles Conservation Area in Sri Lanka. High prevalence of forest die-back patches is also reported in these forests, prompting speculation that there is a connection between bamboo over-abundance and forest die-back. © Tharanga Wijewickrama.

are increased, they start competing with trees for resources, eventually causing their untimely death (Schnitzer and Bongers, 2002; Schnitzer and Carson, 2010). In favor, Wijewickrama *et al*. (2020) observed a higher prevalence of lianas in bamboo-rich forests in Sri Lanka, where high tree mortality incidences were also recorded in comparison to nearby non-bamboo forests.

Ecosystem functions

The bamboo-driven impacts are not only confined to the above-ground features of the vegetation but also on ecosystem functions, such as natural regeneration, decomposition rates and nutrient cycling (Liu *et al*., 2000; Parsons and Congdon, 2008). However, as mentioned previously, comparatively less number of studies has been carried out to explore impacts on ecosystem functions following bamboo over-dominance (Bona *et al*., 2020).

Nutrient cycling

Exotic invaders are known to modify soil nutrient pools and their dynamics through altered litter production, litter quality and decomposition rates (Harner *et al*., 2009; Sharma and Raghubanshi 2009; Piyasinghe *et al*., 2019). However, similar studies lack on 'native invaders' (Bai *et al*., 2016). Litter production, quality and decomposition, and decomposer communities are known to impose overriding impacts on nutrient cycling processes in communities. Exotic invaders produce high quality and quantity of litter, with a high chance of influencing nutrient dynamics (Liao *et al*., 2008; Kurokawa *et al*., 2010; Zhang *et al*., 2013). In contrast, native invaders including bamboos produce poor quality litter compared to that of broadleaved species (Liu *et al*., 2000; Fukushima *et al*., 2015; Song *et al*., 2016), thus anticipating impacts different to that of exotic counterparts. Apart from mass die-off events, bamboo-dominated forests recorded a lower litter production (in terms of dry weight basis) in comparison to adjacent broadleaved forests (Song *et al*., 2016; Wijewickrama *et al*., 2021). During mass die-off events, bamboos produce large amounts of litter thereby causing significant impacts on biogeochemical cycles and nutrient pools.

Liu *et al*. (2013) observed a higher soil total N content in bamboo forests than that in evergreen broadleaved forests. In contrast, Song *et al.* (2017) observed a decelerated nitrogen cycle in an evergreen broadleaved forest in the sub-tropical China following a native bamboo invasion (*Phyllostachys pubescen*s), indicating a risk of decline in soil fertility status over time. Shen (2015) observed an increased nitrogen mineralization and nitrification following a spread of bamboo in a broadleaved forest. These conflicting findings suggest the importance of further deliberations on bamboo-driven nutrient cycling processes through comprehensive research. Austin and Marchesini (2012) observed a negative impact on carbon and nutrient cycles due to slow decay of bamboo litter, confirming the crucial role of decaying rates on nutrient dynamics (Fujimaki *et al*., 2008; Tu *et al*., 2014; Song *et al*., 2016). Other studies also observed poor mass losses in bamboo litter compared to that of broadleaved forest species (Liu *et al*., 2000; Tripathi *et al*., 2006; Fujimaki *et al*., 2008). Overall, low quality and quantity of litter together with diminished decomposition rates can instill negative impacts on biogeochemical cycles following bamboo invasions.

Biotic interactions

Seed dispersal mechanisms are decisive factors in determining plant composition and diversity in forests. Plants provide resources for seed dispersers thus any constraints to seed dispersal mechanisms could jeopardize the natural succession of forests (Holl, 1999). In addition, the availability, quantity and richness of the seed rain are key factors maintaining the natural regeneration process. The bamboo-induced changes to light levels in the forest floor and their mass flowering and die-off events could alter trophic interactions including seed dispersal, predation and herbivory (Kitzberger *et al*., 2007; Giordano *et al*., 2009; Marchesini *et al*., 2009). In a recent study by Bona *et al*. (2020), a low seed richness was observed in bamboo-dominated forests (a native bamboo, *Guadua weberbaueri*) that would eventually lead to notable compositional differences among bamboo- and bamboo-free forests.

Forest regeneration

Bamboos influence the natural regeneration in two different ways; (i) through changes in micro-habitat caused by over-dominance and (ii) changes caused by their unusual fruiting events followed by mass die-offs. Oddly, both scenarios alter micro-environmental conditions in the forest interior in conflicting ways. As an example, the over-dominance of bamboos may reduce the light intensity in the forest interior while the mass die-offs would increase it. These conflicting modifications affect the natural regeneration in the forest, deviating from its normal trajectory and incurring long-lasting changes in the forest structure. Furthermore, soil seed bank and seedling recruitment may also use as evidence to predict changes to regeneration potential (Vandvik *et al*., 2016), though few studies have been carried out in forests invaded by native bamboos (Wijewickarama *et al*., unpublished).

Prematilleke *et al.* (2008, 2015) reported that *Ochlandra stridula*, an endemic bamboo species in the wet zone of Sri Lanka, hinders forest regeneration due to its rapid expansion (Figure 1). This is the first account in the country raising awareness on potential threats of 'native' invaders to forest communities. This work attracted criticisms from the scientific community as the focal plant is an 'endemic' instead of an 'exotic', which has challenged the 'norm'. However, since then, more studies have been undertaken globally acknowledging that even native/endemic plants could become invasive in their home ranges bringing negative consequences, perhaps similar to exotic invaders (Pivello *et al*., 2018).

Shading effect, physical damage to saplings, exposure to frequent fires and heavy litter accumulation have been proposed as possible causes for the decline in regeneration potential (especially trees) in bamboo-dominated forests (Oliveira-Filho *et al*., 1994; Silman *et al*., 2003; Griscom and Ashton, 2006). Woody bamboos are known to influence the forest structure and dynamics by casting a shade on the forest understory (Guilherme *et al*., 2004), while at the same time providing a favourable micro-habitat for seed predators (Iida, 2004). Low sunlight in the forest understory and high incidence of seed predators may incur negative influence on tree seedling recruitment, growth and their survival, with the possibility of disturbing the natural forest succession (Griscom and Ashton, 2003; Campenello *et al*., 2007). Due to the absence of fleshy fruits, bamboos attract less seed dispersers which could also influence the seed rain negatively. In Brazil, a severe inadequacy of seeds was noted in bamboo-dominated forests over non-bamboo forest stands explaining the poor seedling recruitment in the latter (Rother *et al*., 2009). In contrast, a study carried out in Sri Lanka observed that *B. bambos*-dominated forest patches had more seedlings but with the least representation from tree seedlings (Wijewickrama *et al*., 2021). Rother *et al*. (2018) too observed a higher seedling abundance and emergence under the bamboo canopy than of forests without bamboo, though the diversity is less. These findings further support the tendency shown by bamboo-dominated forests to modify their species composition and structure over time.

As bamboos tend to grow fast and produce high biomass, bamboo-rich forests get more litter (in terms of the thickness of the litter layer) in comparison to broadleaved native forests. Surface litter may incur contrasting impacts in the forest regeneration potential based on species-specific requirements (Larpkern *et al*., 2011; Rother *et al*., 2016). A thick litter layer may inhibit seed germination due to lack of sunlight (Facelli and Picket, 1991), and at the same time, increasing the abundance of pathogenic fungi due to improved humidity (García-Guzmán and Benítez-Malvido, 2003). The accumulation of light-weighted bamboo litter may also increase the risk of forest fires especially during dry periods (Wijewickrama *et al*., 2019), incurring detrimental impacts on emerging seedlings. Massive flowering followed by mass dieback events in bamboo may also influence the natural regeneration (Gonzalez *et al*., 2002; Rother *et al*., 2009), through modifying germination rates and seedling mortality (Brokaw and Busing, 2000; Budke *et al*., 2010). Mass death events in bamboo alter micro-environmental conditions markedly, in terms of light and temperature, which are considered as decisive factors influencing the regeneration process (Budke *et al*., 2010; Capellosso *et al*., 2016).

Edaphic properties

Soil nutrients

Invasion driven changes to edaphic properties are under-studied in comparison to above-ground parameters (Millangoda and Madawala, 2018). In plant communities, the litter production, litter chemistry and their decay rates are overriding factors that determine changes in soil nutrients over time (Giebelmann *et al*. 2013). Bai *et al.* (2016) reported a decrease in soil organic carbon and nitrogen in upper soil layers following bamboo dominance in a study carried out in Southern China, while others noted an increase in N (Chang and Chiu, 2015; Chang *et al*., 2018). Poor quality and low production of bamboo litter are identified as factors responsible for decrease in N mineralization rates thus causing a low availability of soil N (Song *et al*., 2016). In contrast, others demonstrated an increase in soil organic C and N following bamboo expansion (Wu *et al*., 2008; Song *et al*., 2013; Wang *et al*., 2017), indicating the lack of consistency in findings. Wijewickarama (2020) observed no marked changes to soil nutrients in a comparative study carried out in bamboo and non-bamboo forest patches located in the intermediate climatic zone in Sri Lanka. These conflicting results question the ability of some bamboo species to change the soil nutrient status while others tend to colonize preferably in nutrient-rich soils. In a seedling assay carried out with *Ricinus communis*, seedlings performed better in bamboo soils than that of non-bamboo soils further speculating the ability of bamboos either to enhance the soil fertility status or establish specially on nutrient-rich soils (Millangoda and Madawala, 2018). Liu *et al*. (2019) rightly discouraged the oversimplification of bamboo impacts on soils as the severity and the time duration of the invasion, together with other site-specific inherent factors may vary between communities and sites.

Soil microbes

Soil microbes are major drivers of soil nutrient dynamics and are sensitive to vegetation-driven changes (Xu *et al*., 2020). The intimate relationship between the above-ground vegetation and the below-ground microbiota is rather a well-established fact highlighted by scientists. Accordingly, any changes to the above-ground vegetation could trigger comparable changes to the below-ground communities. Exotic invaders have shown to alter the structure, composition and richness of soil microbes (Madawala, 2014; Stefanowicz *et al*., 2019; Bani *et al*., 2018; Mafaziya *et al*., 2019). Despite having ample evidence to suggest that exotic invaders modify soil microbiota, fairly few studies are available to explore potential impacts of native invaders

(Xu *et al*., 2014; Xu *et al*., 2015; Mafaziya *et al*., 2019; Tian *et al*., 2020). The limited number of studies done on bamboo-driven influence on soil microbes indicate somewhat contradictory findings to that of exotic invaders. Interestingly, a study carried out in bamboo-invaded native forests in China has shown that *moso* bamboo dominance has increased the microbial biomass and taxonomic diversity despite a decrease in above-ground diversity (Xu *et al*., 2015). In favour, a study carried out in Sri Lanka witnessed a higher abundance and richness of AMF following a population expansion of native *B. bambos*, with no apparent changes to its community structure (Mafaziya *et al*., 2019). Tian *et al*. (2020) observed a decline in fungal diversity following a *moso* bamboo invasion in a subtropical forest in China, with no marked impact on the bacterial diversity, suggesting that fungi be more sensitive to bamboo invasions than its bacterial counterparts. However, the limited studies may not allow reaching any solid conclusions on how bamboos modify soil microbial populations.

Fauna

There is evidence to believe that single-species dominance could alter the richness and distribution of many critical faunal groups. Watling *et al.* (2011) reported that a native frog species, *Lithobates clamitans,* has been adversely affected after altering the micro-climate following the shrub invasion of *Lonicera maackii*. A meta-analysis also confirmed comparable findings in terms of arthropods (Hengstum *et al.*, 2014). Invasions are known to impose behavioral changes in native animals through interference/competition, heightened risk of predation and modifying habitats (Byers, 2000; Tuomainen and Candolin, 2011). In parallel, when a native invader expands its population in a hasty manner at the expense of other co-occurring species, similar effects could also be anticipated on native fauna. Being a major component in forests, bamboos provide food and shelter for many animals, including one of the most endangered species on earth, the giant panda (Schaller *et al*., 1985; Pan *et al*., 2001) and providing evidence for their long history in the co-evolution.

The mass dieback event in bamboo may also threaten some animal species that exclusively depend on them. Giant panda (*Ailuropoda melanoleuca*), red panda (*Ailurus fulgens*), the Himalayan black bear (*Selenarctos thibenatus*) and the smallest known bat (*Tyloncteris pachypus*) are some known animals that depend solely on bamboos for their nourishment and survival (Bystriakova *et al*., 2003). Furthermore, more than 15 rare and threatened bird species in Asia have chosen bamboos exclusively as their roosting habitat (BirdLife International, 2000). Such specialized relationships between animals and bamboos highlight the subtle balance between them.

Yang *et al*. (2008) observed a drastic reduction in richness and abundance of birds in a native broadleaved forest following a bamboo invasion. In contrast, a study conducted in Brazil showed an increase in the avifaunal richness following an expansion of a native bamboo species (*Guadua tagoara*), possibly due to the sudden availability of ample food and perches (Rother *et al*., 2013). The high heterogeneous environment in bamboo forests due to their patchy distribution seems to favor the avian population. The scarcity of studies and existing contradictory findings are major hindrances to reach solid conclusions in bamboo-driven impacts on fauna.

Mass death events in bamboo forests can lead to create gaps in forests triggering significant changes in the micro-climate of the forest undergrowth (Campanello *et al*., 2007; Budke *et al*., 2010; Montii *et al*., 2011; Capellesso *et al*., 2016). Ground-dwelling insects are highly sensitive to environment and substrate modifications (Moldenke *et al.,* 2000). As arthropods thrive on specific substrates for feeding and breeding, any changes to above-ground vegetation may incur significant changes to the composition and structure of litter-dwelling arthropods (Bernays and Graham, 1988). The potential bamboo-driven changes to micro-environment of the forest floor (light intensity, temperature, and soil moisture) could trigger changes in the mobility, distribution and reproductive success of litter-dwelling arthropods (Wolkovich *et al*., 2009; Talley *et al*., 2012). A study conducted in Sri Lanka also confirms that *B. bambos* spread has increased the abundance and richness of litter-dwelling arthropods perhaps due to the sudden availability of a suitable substrate for their sustenance and survival (Wijewickrama *et al*., unpublished). Therefore, sudden expansion of native bamboo populations and their die offs may cause a significant influence on ground-dwelling faunal groups (Davidson *et al*., 2006; Jacobs *et al*., 2018), but the lack of research restraints in reaching firm generalizations. The impacts of bamboo on soil fauna and their interactions seem to vary among faunal groups (Liu *et al*., 2021), further reiterating the necessity of more studies.

Bamboo-dominated forests: their management

Similar to 'exotic' invaders causing serious environmental and societal issues worldwide, the 'native invaders' have also laid down grave challenges to scientists, conservationists, policymakers, and the communities living close to these forests. However, due to many reasons, this issue has not been given due recognition by the authorities. Therefore, the scientific knowledge on 'native' invaders is mandatory outside the existing knowledge on 'exotic' invaders in order to find answers to their exclusive life traits that facilitate their ability to invade home ranges and to introduce new strategies to manage them effectively. As 'native' invaders have many economic uses, controlling, and managing them could pose added challenges unlike the 'exotic' invaders, which are well-known for their damaging impacts. As they are 'natives', it is still not clear whether they can cause long-term detrimental impacts on their home ranges or their impacts are short-lived. Thus, short-term as well as long-term studies are imperative to understand their life traits and potential behaviours. However, making the general public and communities aware of potential threats of 'native' invaders could be a crucial step towards getting rid of societal challenges before prioritizing goals and earmarking management strategies.

Figure 7: A plantation of *Bambusa balcooa* (a native clumping bamboo species) in India. It intercrops with mustard (inset). *B. balcooa* has many commercial uses including wood chip industry, building material, raw material for fishing and agricultural implements, paper pulp etc. Shoots are consumed as a vegetable and leaves as a fodder. © Prof. Salil Thewari, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India.

It is startling to observe the gradual increase of bamboo forests while the native forest cover declines at a steady annual rate (Ferreira *et al.,* 2020). Some countries introduce bamboo plantations to use as a renewable resource, and for other ecological and economic returns. Therefore, careful planning and management interventions are imperative when establishing 'exotic' or 'native' bamboo species for commercial use. The management and mitigation measures of 'exotic' invasions have been amply evaluated and tested under different habitat and climatic conditions. However, a comparable attention has not been given for 'native' invaders. Despite possible similarities in their likely impacts ('exotic' and 'native' invaders), comparable approaches may not be feasible due to marked differences in their ecological status, other life traits and possible impacts. Therefore, specific management interventions need to be identified for 'native' invaders and tested under different field and climatic conditions before use them in large-scale missions.

Unlike other 'native' invaders, bamboos are extremely adaptable and competitive, making them good contenders for invading fragile habitats. Their ability to spread through rhizomatous growth adds a new dimension to this problem. Therefore, imposing physical barriers can be considered as an effective measure to restrain their expansion through clonal growth (Isagi and Torii, 1997). However, erecting physical barriers could only be feasible for small-scale bamboo plantations or forests. A success story is reported from China where the bamboo spread is controlled through manual methods (Ying *et al*., 2016; Kudo *et al*., 2017), in a trial carried out in small experimental plots. Therefore, similar outcomes cannot be anticipated from large-scale areas due to the innate vigor of bamboo species and other practicalities. The selection of bamboo species with low invasive potential, avoiding susceptible areas, implementing measures to stall expansion and encouraging mix planting are some of the measures to contemplate when introducing bamboo plantations, though some of these management interventions are labour intensive and costly [(Brown *et al*., 1987; Li *et al*., 2003), Figure 7].

Bamboo forests possess a low timber potential, thus any logging activities need caution (D'Oliveira *et al*., 2004; Rockwell *et al*., 2014). The lack of scientific data and due recognition of the issue are major impediments of introducing effective strategies to manage native bamboo invaders (Rockwell *et al*., 2014; Buziquia *et al*., 2019). The lack of comprehensive studies on native bamboo invaders is perhaps due to either strain of carrying out vegetation studies in bamboo-rich forests and/or poor recognition of bamboo-rich forests from the rest of the forest types (Griscom, 2003; Phillips *et al*., 2003). In some countries including Sri Lanka, the bamboo invasion is highly localized, thus can be easily evaded the necessary attention from the researchers and policy makers. Some countries in the region generally highlight the positive consequences of bamboo forests more than the negative, while emphasizing its place in the high conservation priority (Tuanmu *et al*., 2013). Others highlight the economic values of bamboo forests and their role in alleviating environmental issues, such as soil erosion, water conservation, land rehabilitation and carbon sequestration (Zhou *et al*., 2005). Therefore, the negative aspects of bamboo dominance are largely concealed by their more renowned ecological and economic returns, prompting more challenges to address this issue. During the past decade, more studies have come to the forefront highlighting their negative ecological impacts in their introduced/native ranges and their discreet ability to invade adjoining landscape, suggesting physical removal as the only solution to restrain those (Bai *et al*., 2013).

In order to exploit bamboo resources in a sustainable manner while introducing effective management strategies, it is crucial to know their extent of distribution (Yang *et al*., 2016). The quantification of bamboo resources is also important as they have many economic uses. A study conducted in Western Ghats in India to explore spatial and temporal trends of a native reed bamboo population of *Ochlandra travancorica* is reported that nearly 21% of bordering evergreen forests has been transformed into pure bamboo stands over the years (Dutta and Reddy, 2016), highlighting the severity of the problem. These alarming findings prompt the importance of long-term monitoring of growth and spread of bamboos using techniques such as GIS and remote sensing, to ensure tracking their expansion in a more effective manner.

Overall, baseline information on bamboos, their extent and distribution, and potential impacts are lacking, challenging their effective control and sustainable management. Therefore, further research is required to fill the existing knowledge gaps on invasive bamboos and their potential impacts in order to find solutions to their adverse consequences. Climate-driven responses and adaptations, characteristics of bamboo-forest interface, inherent traits, and underlying mechanisms in facilitating bamboo expansion are some of the crucial areas that need more scientific knowledge to explain their unusual behaviour in native forests (Yang *et al*., 2015; Buziquia *et al*., 2019), and to bring effective measures to control them. Larpkern and Totland (2011) hypothesized that the impacts of bamboo on co-occurring species may differ depend on the bamboo species and their major climatic zones, further supporting the importance of more comprehensive studies under different climate-habitat conditions to understand precise driving forces behind bamboo invasions. In countries where bamboos introduce as plantations need sturdy actions to monitor their growth to avoid any potential encroachments into nearby areas (Buziquia *et al*., 2019), as once they escape territories, controlling them would be rather difficult due to their robust nature.

Knowledge gaps, challenges, and future ahead

This review identified many knowledge gaps in native bamboos with invasive traits and challenges in controlling and managing their potentially less-known consequences. In addition to the basic understanding of invasive bamboos, the details of their expansion process and its underlying mechanisms, risk evaluation and management, and control strategies still lack appropriate focus and direction. It is not feasible to rely solely on information gathered on ‘exotic’ invasive species to address the potential consequences of ‘native’ invaders as their life traits, respective mechanisms and driving forces seem to differ considerably. Therefore, it is of great importance that scientists put more collective and concerted effort in identifying the exclusive behavior of ‘native’ invaders under different bio-climatic zones. In addition, the sustainable utilization of bamboo resources also needs due attention as it is probably the most effective and sustainable way of managing them without incurring major monetary constrains, especially in countries with poor economies (Figure 8).

Though there is sufficient evidence to show that native bamboos have the potential to expand their territories under unknown circumstances, there is a dearth of information to predict their impacts under different habitat-climate settings and also to ascertain what trigger their sudden change in growth. The lack of taxonomic-driven research in bamboo-dominated forests also makes it hard to acquire an overall depiction about their potential impacts. Up to now, the available research on native bamboo invaders has been mostly confined to the South

Figure 8: A: *Phyllostachys* sp. (a running bamboo) at Doi Chang Buddhist Park, Chiang Rai, Thailand; B: *Dendrocalamus* sp. (a clump forming) bamboo in Mae Fah Luang, Chiang Rai, Thailand. © Binu Samarakoon, Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai, Thailand.

American sub-continent, China and Japan, thus making the current knowledge inconsistent and sporadic.

As a step forward, it is crucial to map the distribution of bamboo-dominated forests though it could be a major challenge to countries with low economic promise. Remote sensing (RS) and GIS are rapid and relatively accurate methods to map and quantify the distribution of natural resources. However, estimating the extent of bamboo-dominated forests is a challenging task as they grow dispersed and intermingled with other species in the forest understory with only some species reaching the canopy level (Lobovikov *et al*. 2007; Wang *et al*., 2009). These may limit the use of GIS and RS in mapping the distribution bamboo invaders (Dida *et al*., 2021). The application of RS in bamboo forests is rather complicated not only due to their scattered distribution but also due to the difficulty in separating them from other co-occurring forest species. There were few studies where expensive, high resolution satellite images are being used in detecting bamboos with sufficient ground-truthing (Ghosh and Joshi, 2014). In contrast, others claimed that bamboos, being an evergreen plant, could be easily detected and quantified using RS especially in the winter or in the dry season when other trees lose their green colour due to leaf senescence (Ferreira *et al*., 2020). Despite these challenges, there are some promising trials carried out in countries, such as China, India and Brazil, to quantify bamboo forests using RS (Bharadwaj *et al*., 2003; Linderman *et al*., 2004; Tang *et al*., 2016). Dida *et al*. (2021) carried out an extensive study to quantify bamboo resources in the Philippines, but omitting those in the forest understory due to low visibility and limited inventory data for validation. FAO (2005) highlighted the lack of consistency in terms of the quality and the reliability of data on the distribution of bamboos among countries. However, countries from the Asia-Pacific region have more accurate and comprehensive data on the distribution of bamboo forests compared to that of Latin America and Africa. Overall, the statistics related to bamboos are inconsistent due to the (i) lack of systematic inventories, methodologies and techniques, (ii) their position as an understory species, (iii) lack of records due to local trade, and (iv) incompatible definitions of ‘bamboo forests’ among countries (Dida *et al*., 2021). Therefore, more steps are needed to aptly identify and categorize bamboo forests, and more studies are to be conducted to fill some of these crucial knowledge gaps to face specific challenges.

The historical information to track the chronology of bamboo expansion is crucial to demonstrate how and when a ‘native’ species transformed into a ‘native invader’ over time (Carey *et al*., 2012). However, historical data on bamboos are generally lacking in many countries that limits identifying what climatic factors or human/natural disturbances trigger their sudden expansion. Furthermore, the impacts of native bamboos on other populations, communities and ecosystems have not been systematically documented. Thus, studies to explore their short- and long-term impacts on biotic and abiotic factors of their respective native ranges are needed to cover as many climate-habitat combinations as possible. This information is imperative to draw the public interest in this issue and its consequences, and to introduce tangible management practices. The factors that trigger the expansion of native bamboo populations and their underlying mechanisms also need further attention by researchers. Some argue that direct human-mediated disturbances may trigger their invasive behavior, while others debate that these abrupt events are driven by climate change, fire, etc. (IPCC Climate Change, 2007). However, few studies emphasized that bamboos expand their populations unaided by human activities (Bai *et al*., 2016), prompting further deliberations to find evidence behind the unusual behavior of native invaders.

Inferences

Approximately a decade ago, native invasions are never heard of due to misfits in definitions. However, this issue gains momentum after recognizing the fact that native species too can become invasive in their home ranges triggered by some factors unknown to the scientific community yet. The growing scientific information on native bamboos with invasive behaviour indicates the seriousness of this issue with statistics to prove that bamboo-dominated forests are increasing at an alarming rate in a global scale. However, the lack of systematic studies on native bamboo invaders and their impacts on ecosystems sets a serious setback in managing them in a sustainable manner. The available scientific evidence suggests that bamboo over-dominance impose serious ecological impacts on biodiversity and vital ecosystem functions in their home ranges that may eventually lead to permanent modifications to resident communities over time. These effects may inflict long-term influences causing irreversible structural and compositional changes in forest communities. Many disparities in available evidence on bamboo-driven impacts suggest the gravity of oversimplification, thus highlighting the importance of comprehensive studies to cover all habitat-climate combinations. The importance of exploring the bamboo-driven impacts on below-ground resources is also highlighted. Lack of scientific and historical information is a major challenge towards introducing effective management strategies to curtail any detrimental impacts of bamboo dominance. The review highlights the arbitrary nature of scientific information and the importance of conducting further studies to fill crucial knowledge gaps on native bamboos. Introducing strategies to manage and control their harmful impacts is a crucial next step after resolving the initial challenges posed by native bamboos displaying invasive traits.

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DECLARATION OF CONFLICT OF INTEREST

The authors declare that the paper does not contain any conflict of interest.

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