

**Review article**

Impact of plant invasion on physical, chemical and biological aspects of ecosystems: A review

**Parvaiz Ahmad Lone, Javid Ahmad Dar, Kothandaraman Subashree, Debojyoti Raha,
Praveen Kumar Pandey, Tapas Ray, Pramod Kumar Khare
and Mohammed Latif Khan***

Biodiversity Conservation Division, Department of Botany, Dr. Harisingh Gour Central University Sagar,
Madhya Pradesh-470003, India

*Corresponding Author: khanml@yahoo.com, khanml61@gmail.com

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Abstract: Biological invasion is considered as one of the major threats to native ecosystems. Here, we review the impacts of invasive plants on the physical, chemical and biological aspects of ecosystem functioning. Introduction of invasive plants impact ecosystems profoundly in a multitude of ways by modifying the physical (soil temperature, soil moisture, etc.), chemical (elemental composition, litter dynamics, nutrient cycles, allelopathy, etc.) and biological components (plant community structure, soil microbial biota and fauna). Most studies have shown a negative feedback of biological invasion on the physical, chemical and biological aspects of the ecosystems. Very often, a positive feedback has been generated between the physico-chemical and biological aspects that favour invasion success. Hence, the in-depth and long-term monitoring is needed to focus on the impact of invasive plants on the species diversity, soil biogeochemistry for better understanding of plant invasion processes in ecosystems, so that proper management strategies could be developed for combating the negative impacts of plant invasion.

Keywords: Exotic plants - Native ecosystems - Community structure - Biogeochemistry - Litter dynamics - Micro biota.

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INTRODUCTION

Biological invasion is a global problem that threatens natural ecosystems. It is the second-largest threat (after habitat destruction) to biodiversity (Drake *et al.* 2003, Wekhanya 2016) and is one of the major drivers of global change (Sardans *et al.* 2017). By definition, invasive species refers to those organisms that have moved from their native habitat to a new location, where they cause significant harm to the environment, economic systems and/or human health (Richardson *et al.* 2000, Tiwari 2005, Beck *et al.* 2008). In other words, invasive alien species are those species whose ranges have been altered either unintentionally (such as accidental introductions) or intentionally (such as purposeful introductions) by humans. This results in self-replacing populations over several life cycles and thus spread over large areas in the new habitat (Pyšek & Richardson 2010, Richardson & Rejmánek 2011, Abrahams *et al.* 2019). A successful biological invasion is one in which the alien species is capable of overcoming abiotic and biotic barriers and establishing self-sustaining populations (called naturalization) for a considerable distance away from the original place of introduction along the introduction-naturalization-invasion continuum (Richardson *et al.* 2000, Richardson & Pyšek 2012, Gioria & Osborne 2014). They occur in practically all kinds of terrestrial ecosystems (Vitousek 1994) and comprise 20% or more of the continental flora and 50% or more of the island flora (Seabloom *et al.* 2006, Sardans *et al.* 2017). Among the different kinds of terrestrial ecosystems, montane ecosystems are considered to be at the lower risk of plant invasions due to the various ecological filters faced by the mountains as they move along high altitudes (Pauchard *et al.* 2009, Alexander *et al.* 2011, McDougall *et al.* 2011, Pathak *et al.* 2019).

Invasive species typically are more tolerant than the native species to a wide range of environmental conditions and possess unique biological traits that offer them various competitive advantages (Sundarapandian *et al.* 2015, Sundarapandian & Subashree 2017). Their widespread establishment could be attributed to their performance-related traits such as physiology, growth rates, shoot allocation, leaf-area allocation, size and fitness, etc. (Liao *et al.* 2008, van Kleunen *et al.* 2010, Stefanowicz *et al.* 2018). In addition, invasion success is also favoured by various other factors explained by hypotheses such as ‘enemy release’, ‘empty niche’, ‘resource availability’, ‘novel weapons’, ‘disturbance hypothesis’, etc. (Dar *et al.* 2019).

As per the International Union for Conservation of Nature (IUCN 2004), the impacts caused by the invasion of exotic species are usually immense, insidious and irreversible (Wekhanya 2016). They may colonize and dominate an urban area or a region of wilderness; particular land-use habitats or protected areas (Wekhanya 2016). The impacts caused by them are often categorized as follows: economic, social and environmental. Economic impacts are those consequences in which humans face direct monetary losses. Social impacts are those in which the human health or safety or other aspects of social culture are affected. Environmental impacts are those in which the ecosystem processes are affected leading to the loss of biodiversity and ecological functionality (Charles & Dukes 2008, Wekhanya 2016). The rapid expansion of the invasive plant species with/without human influence has resulted in drastic modifications of natural ecosystems, threatening various ecosystem functions and services (Gordon 1998, Uddin & Robbinson 2017). The invasion of exotic plant species could change entire ecosystems by altering physical, chemical and biological properties of the habitat, communities and ecosystems, by altering fire regimes, hydrology, nutrient cycling and other ecological processes (Pathak *et al.* 2019). The introduction of a new species in a new area exerts a great effect on the structure and/or ecosystem functioning. Such effects/impacts may be manifested at the level of populations or communities in the early stages of invasion and at an ecosystem-level at a later stage. While some impacts may be rapid and dramatic, others may be expressed slowly (Brooks *et al.* 2004, Pyšek & Richardson 2010). Invasive species can induce changes in the ecosystem cycles such as water, carbon, nitrogen, etc. and affect soil nutrient dynamics, besides altering the biogeochemistry, geomorphology, hydrology and disturbance levels in ecosystems (Gordon 1998, Ehrenfeld 2003, Yadav *et al.* 2016, Dutta 2018). Simultaneous invasion by different invasive plant species could drastically alter the three-dimensional structure of forests (Asner *et al.* 2008, Kumari & Choudhary 2016, Dutta 2018). Invasive plant species were also reported to form monospecific strands by outcompeting the native plant species, bringing about a great loss in plant diversity (Gaertner *et al.* 2009, Powell *et al.* 2011). The various threats posed by plant invasion to ecosystems could be summarized as: habitat loss, biodiversity decline, changes in litter quality, quantity and decomposition rates, soil physico-chemical properties, soil biota, etc. (Theoharides & Dukes 2007, Vilà *et al.* 2011, Dassonville *et al.* 2011, Sanon *et al.* 2012, Wang *et al.* 2015, Kumari & Choudhary 2016). It is important to note that invasive plants exhibit different degrees of invasion in the affected areas (Theoharides & Dukes 2007, Si *et al.* 2013) and the impacts may vary across local conditions, different seasons, soil type and the nature of the native community (Ehrenfeld 2003, Bjerknes *et al.* 2007, Dutta 2018).

Successful establishment of an invasive species could exacerbate the impacts of invasiveness by a phenomenon called ‘invasional meltdown’, which is caused by the co-facilitation of multiple invasive species, which might result in a ‘stable degraded state’ as in a grassland agro-ecosystem (Kulmatiski 2006, Best & Arcese 2009, Jordan *et al.* 2011, Dar *et al.* 2019). As the globalization proceeds at a rapid pace, the number of alien species getting introduced into new areas continues to rise (van Kleunen *et al.* 2015, Helsen *et al.* 2018). The spread of invasive plant species has been reported to increase with trade, travel and technology and they have now colonized even forests, which were once considered to be low-risk areas (Meyerson & Mooney 2007). Biological invasions have increased worldwide as invasive species could act as both ‘drivers’, by outcompeting and dominating the native species with their unique eco-physiological traits and abilities and ‘passengers’, by dominating a region as a consequence of anthropogenic actions such as environmental degradation, habitat fragmentation, global climate change, etc. (Powell *et al.* 2011, Dar *et al.* 2019). Assessment of the impacts of invasion is a major task in invasion science (Bartz & Kowarik 2019) and the various ecological and economic losses caused by biological invasions have propelled various authorities to frame several policies and take management and restoration operations. As the plant-soil feedback interactions are induced by invasiveness via physico-chemical and biological mechanisms, it becomes important to understand the impacts of invasion on physical, chemical and biological aspects of ecosystems. This review aims to understand the various impacts of plant invasion on physical, chemical and biological aspects of ecosystems from various literary sources. The method of literature selection was done using the search terms “invasive plants”, “biological invasion of plants”,

“native versus invaded ecosystems”, “impact of plant invasion on physical aspects of ecosystems”, “impact of plant invasion on chemical aspectsof ecosystems” and “impact of plant invasion on biological aspectsof ecosystems” in different search engines such as Google Scholar, Scopus and Web of Science.

IMPACTS OF INVASION ON PHYSICAL ASPECTS

Plant invasions alter the physical properties of the ecosystem in many ways, especially that of soil. Invasive species also alter the patterns of energy flow in trophic level interactions, food chains and food webs (Wekhanya 2016). The invasive species are well-known to modify the physical habitat as well by intensifying the disturbance regimes such as flooding, soil erosion and forest fires. Invasion by *Lantana camara* L. is known to alter fuel loads and a positive feedback exists with forest fires, constituting the fire-lantana cycle (Hiremath & Sundaram 2005). Forest fire cycles could be influenced in different ways as for example when grasses invade shrublands, fire frequency and intensity are enhanced, whereas when trees invade grasslands, fire suppression occurs (Wekhanya 2016). Plant invasion can have a drastic effect on the physical environment by altering the rates of both carbon dioxide emission and sequestration and/or by the emission of volatile organic compounds as well as biologically important gases (Dukes & Mooney 2004, Charles & Dukes 2008).

Several invasive plant species are known to modify soil properties, which would favour their own development and propagation (van Breemen & Finzi 1998). Many studies have reported that native species thrive well in native soil than the invaded soil, which indicates that the soil properties are altered when an invasive species is introduced in a new habitat (Ehrenfeld 2003, Sharma & Raghubanshi 2011, Simba *et al.* 2013). Invasive species alter the physical habitat as well as soil properties such as surface soil temperatures, hydrological processes, etc. By influencing the abiotic and the biotic properties of the soil, invasive plants alter the soil's ability to support the same individuals or other individuals of the same invader species or other plant species and such interactions are known as ‘plant-soil feedbacks’, which play a crucial role in invasiveness (Ehrenfeld *et al.* 2005, Kulmatiski & Kardol 2008, van der Putten *et al.* 2013). Invasive plant species can also make the soil less suitable for other species to grow by secreting salts increasing the soil salinity [*e.g.* *Tamarix ramosissima* Ledeb. (Zavaleta 2000) and *Mesembryanthemum crystallinum* L. (Vivrette & Muller 1977) or by acidifying the soil (Callaway & Ridenour 2004, Charles & Dukes 2008, Wekhanya 2016)].

As invasion takes over in a new habitat, the community structure of the ecosystem gets altered, which in turn changes the surface soil properties such as soil water and nutrient absorption capacities, heat capacity, soil temperature, etc., which would in turn affect root and shoot development of seedlings and saplings (Oades 1984, Hamblin 1986, Smith *et al.* 1987, Singh & Sainju 1998, Gibbons *et al.* 2017, Stefanowicz *et al.* 2018, Caspi *et al.* 2019). Alteration in plant community structure also causes significant changes in soil properties such as water-holding potential and soil porosity. Changes in root characteristics are known to affect the soil pore size, pore distribution and pore continuity, which would in turn influence the hydraulic conductivity of the soil (Hamblin 1986, Radcliffe & Rasmussen 2002).

Invasive plant species alter the hydrological cycles in the invaded environment via changing the rates and timings of evapotranspiration, runoff as well as water table levels. Such impacts vary with the variation in the invaders' traits such as rooting depth, leaf area index, transpiration rate, tissue biomass and phenology (Levine *et al.* 2003). Alteration in the water cycle would have profound changes in water supply and regulation, which would in turn affect humans (Levine *et al.* 2003, Charles & Dukes 2008). Soil moisture, which is an important soil pool is also affected by the degree of plant invasion and changes in soil moisture due to plant invasion often results in changes in the microbial flora of the rhizosphere in a manner that promotes further invasiveness (Si *et al.* 2013). Soil moisture is a property that is influenced by rooting depth and the season of active uptake (such as summer) and as invasive plants have a deeper rooting depth and are active during different times of the year, soil moisture is affected due to the drawing up of large volumes of soil water (Enloe *et al.* 2004, Potts *et al.* 2008, Ehrenfeld 2010). The rapid growth and long persistence time of invasive plants, which leads to fast evapotranspiration rates, are also important causes for the decrease in soil moisture (Wolf *et al.* 2004, Wang *et al.* 2015). Apart from the rooting depth, the higher evapotranspiration rates are also caused due to larger plant sizes and greater leaf area than the native plant species. A well-known example is the case of *Tamarix* which is known for its ability to alter the water budget and water dynamics of the whole ecosystem due to its large leaf area (Sala *et al.* 1996, Ehrenfeld 2003). Thus, invasive alien plant species alter the physical environment of the invaded ecosystem via various mechanisms.

IMPACTS OF INVASION ON CHEMICAL ASPECTS

Plant invasion has been known to alter the chemical properties of the ecosystem causing considerable

damage to the native biota and thereby ecosystem functions. Invasive plant species affect ecosystems via both direct and indirect effects on soil chemistry (Wekhanya 2016). The root and leaf exudates of the invasive plants affects soil structure, which could mobilize and chelate nutrients and microbial activities (Batten *et al.* 2006, Wekhanya 2016). The impacts of plant invasion on soil's chemical attributes is due to the modification of chemical inputs and patterns of cycling of carbon, nitrogen and other elements, soil organic matter, soil aggregation, soil pH and release of allelopathic substances (Saggar *et al.* 1999, Kourtev *et al.* 2002, Ehrenfeld 2003, Hawkes *et al.* 2005, Thorpe *et al.* 2009, Jordan *et al.* 2011). Invasive plants usually drastically change important soil characteristics such as carbon content, nitrogen content, pH, nitrification rates, mineralization rates and concentrations of important elements such as calcium, magnesium and potassium (Simba *et al.* 2013). The success of invasive plants is often linked with alterations in the soil elemental composition and stoichiometry (Sardans *et al.* 2017).

One of the prominent impacts of plant invasion on the chemical properties of the ecosystem is the alteration in litter and nutrient dynamics of the ecosystem. Invasive plant species affect the various components of the carbon, nitrogen and nutrient cycles, inclusive of aboveground and belowground carbon compounds, net primary productivity, rates of litterfall, quality and quantity of litter as well as rates of nutrient and carbon mineralization (Hector *et al.* 1999, Chapin *et al.* 2000, Ehrenfeld 2003). The changes in the physical properties of the soil also drive changes in the nutrient dynamics (Boettcher & Kalisz 1990, Kelly *et al.* 1998, Ehrenfeld 2001, Ehrenfeld 2003). Nutrient availability to primary producers is an important ecosystem service which is greatly altered when invasion occurs and the plant community structure is altered (Ehrenfeld 2003, Mack & D'Antonio 2003, Dukes & Mooney 2004). The nutrient cycles are influenced by invasive plants through three principal ways: alteration of soil microbial networks, changes in litter disintegration rates and changes in the soil's physico-chemical properties. The primary productivity is key ecosystem functions which could be altered if the ecosystem is invaded by invasive species that utilizes resources more efficiently and cause the elimination of a key native species (Dukes & Mooney 2004). As primary productivity is altered, all other subsequent ecosystem services are also affected. Invasive species exhibit rapid rates of growth have high specific leaf area and accumulate more biomass than the native species (Daehler 2003). The large amounts of biomass accumulated by the invasive plant species differs considerably from that of native vegetation biomass in terms of chemical quality such as elemental composition, lignin content, carbon : nitrogen ratio, lignin : nitrogen ratio and secondary metabolite concentrations (Dassonville *et al.* 2007, Tharayil *et al.* 2013, Stefanowicz *et al.* 2018).

Litterfall and litter decomposition are important ecosystem processes that determine the carbon and nutrient cycles (Couteaux *et al.* 1995, Chen *et al.* 2011; Rai *et al.* 2016). Carbon fixed during photosynthesis is returned to the environment via litter decomposition, which is in turn used for plant development (Sayer 2006, Hobbie 2015). Large amounts of senescent plant biomass reach the soil via litterfall and if the litter quality and the litter decomposition rates are low, litter fragments may form a thick layer, in particular, if the invasive plant species produce less nutrient-rich or more recalcitrant litter than the native vegetation (Ehrenfeld 2003). In some instances, the litter of some invasive plant species exhibits only moderate rates of decomposition due to the presence of secondary metabolites (Boon & Johnstone 1997). Plant invasion drives changes in topsoil chemical composition by uplifting nutrients from deep soil horizons (Dassonville *et al.* 2007, Stefanowicz *et al.* 2018). In other cases, invasive species contain low concentrations of lignin and polyphenolics and high concentrations of nutrients. The litter decomposition rates of these invasive plant litters are very high and nutrients are quickly discharged into the environment expediting nutrient cycles (Allison & Vitousek 2004, Rothstein *et al.* 2004). In such cases, in spite of copious amounts of litterfall, due to rapid decomposition, there is less standing crop litter (Cameron & Spencer 1989). A global meta-analysis by Liao *et al.* (2008) across 94 studies revealed that litter decomposition rates raised upto 117% in the invaded ecosystems, although the rates of litter decomposition might vary across different spatial scales (Wekhanya 2016). The invasive plants could affect leaf litter decomposition directly by changing the quality of leaf litter or indirectly by creating unique conditions in the surrounding environment. The concentration of nitrogen in the litter is an important indicator of litter quality, which also affects the rate of litter decomposition. High-quality litters contain high nitrogen concentration, while low-quality litters contain low nitrogen concentration (Rai *et al.* 2016). Moreover, the leaf litter of invasive plants contains lesser lignin and lower lignin: nitrogen ratios than the native plant species, which accounts for its higher decomposition rates. Leaf litter decomposition and the accompanied release of carbon dioxide and nutrients together with the formation of soil organic matter are the key fundamental processes that influence ecosystem nutrient cycles, carbon flux and humus formation (Wang *et al.* 2011, Zhang *et al.* 2014, Wang *et al.* 2015).

Changes in litter composition and litter decomposition can exhibit marked effects on nutrient cycling. Nutrient cycling is also altered by plant invasion, if colonized by plants that fix nitrogen or if they leach chemicals that inhibit nitrogen fixation or if they release compounds that would affect the ability of nutrient retention (Dukes & Mooney 2004). Nutrient cycling alterations by invasive species often vary in both magnitude and direction depending on the type of invasive species and the invaded habitat. The alteration of nutrient cycling also affects primary productivity and soil fertility (Ehrenfeld 2003). The soils of the ecosystems that were heavily infested with *Lantana camara* L. populations had high concentrations of organic carbon and nitrogen (Sharma & Raghubanshi 2011). The changes caused in nutrient cycling often make the habitat less suitable for the growth of other species (Wekhanya 2016). One often perceived change in nutrient cycling is that the total nitrogen found mostly in organic reservoirs is transformed into various states by means of microbial immobilization and mineralization (Nannipieri *et al.* 2003). The nitrogen cycle plays an important role in successful plant invasions (Theoharides & Dukes 2007, Jones & Chapman 2011, Wang *et al.* 2015). High levels of nitrogen lead to an increase in the biomass of invasive plants and a decrease in the biomass of native plants. This is primarily because invaders are more efficient in resource utilization and have lesser nutrient requirements than the native plant species (Rickey & Anderson 2004, Gurevitch *et al.* 2008, Wang *et al.* 2015).

Invasive plants cause changes to nutrient cycles either dramatically or gradually. The nutrient cycles get altered dramatically when invasive plant species introduce new traits in the ecosystem, which makes resources available from new/unused sources. On the other hand, nutrient cycles are gradually changed when some functional traits possessed by the invasive species induces high rates of nutrient uptake or turnover (Mack *et al.* 2001, Wang *et al.* 2015). Plants principally use two types of nitrogen directly – nitrate nitrogen and ammonium nitrogen. Invasive plants create a microenvironment with increased nitrogen availability that would facilitate further invasion (Hawkes *et al.* 2005, Liao *et al.* 2008, Wang *et al.* 2015).

Soil pH refers to the concentration of hydrogen ions (or protons) in the soil and plant invasion is known to significantly increase the values of soil pH. This could be because invasive plants have high rates of nitrate uptake leading to a decrease in soil nitrite concentration. The decrease in soil nitrite concentration causes a rise in soil pH (Ehrenfeld *et al.* 2001, Fan *et al.* 2010, Si *et al.* 2013). However, the nitrogen acquired by invasive plants can influence soil pH in either way – high ammonium absorption leads to acidification, while high nitrate absorption could cause alkalinization (Kourtev *et al.* 1998, Wang *et al.* 2015). The alteration of soil pH is also dependent on the degree of invasion as in some cases, low degrees of invasion increased soil pH, whereas high degrees of invasion caused no change in soil pH (Si *et al.* 2013, Wang *et al.* 2015). High soil pH is known to increase the rate of litter decomposition and it, therefore, plays a critical role in the regulation of nutrient cycles (Wekhanya 2016).

Alongside the nitrogen cycle, the carbon cycle is also greatly influenced by plant invasion. By altering the plant community structure, invasion by exotic plants alters the aboveground and belowground biomass and thereby carbon stocks. Invasion by woody plants was found to cause about 1.5 fold increase in the soil organic carbon and soil total nitrogen content (Liao *et al.* 2006). The impacts are more pronounced on grassland ecosystems than most other terrestrial ecosystems as grasslands are very susceptible to plant invasion. According to Connin *et al.* (1997), the invasion and subsequent replacement of grasses in grasslands lead to alterations in leaf litter, root mass, soil nutrient availability, soil carbon sequestration and cycling. When the grasslands are invaded by shrubs, the soil organic carbon pool is affected due to the modification of the quality and quantity of carbon sources (Amundson 2001, Jackson *et al.* 2002). However, the impact of plant invasion on carbon cycling is also dependent on other environmental factors. For example, plant invasion was noted to increase the soil organic carbon pool in dry sites while a decrease in soil organic carbon pool was observed in wet sites. The loss of carbon from the soil was found to be greater than the carbon accrued in the phytomass of the wet sites (Jackson *et al.* 2002).

Invasion by exotic plant species greatly affects the biogeochemical pools and fluxes of both matter and energy, which therefore alters the fundamental functions of ecosystems (Ehrenfeld 2010). Soil respiration is a widely measured flux of carbon dioxide from the soil surface. It is a measure of the soil metabolic activity representing the carbon dioxide produced by soil organisms such as microbes, plant roots and fauna. Soil respiration is one of the major causes of carbon loss from the ecosystem (Schlesinger & Andrews 2000). Hence, even a slight shift in soil respiration due to plant invasions could result in great changes in the atmospheric carbon dioxide concentration and the soil carbon pool. Although plant invasions could substantially alter soil respiration rates, researchers have obtained positive, negative and negligible effects. These differences could be attributed to the differences in factors determining soil respiration and different site conditions (Fang &

Moncrieff 2001, McCulley *et al.* 2004, Smith & Johnson 2004, Metcalfe *et al.* 2011).

The impacts of plant invasion on nitrogen and carbon cycles are often well-studied, but the impacts on phosphorous cycle and cations are seldom documented (Ehrenfeld 2010). Invasion by alien plants and soil phosphorous are often correlated (Martin *et al.* 2009). In general, soil phosphorous is found to increase following plant invasions (Duda *et al.* 2003, Hughes & Denslow 2005, Vanderhoeven *et al.* 2006), but some studies noted a decrease or a lack of change in soil phosphorous content (Collins & Jose 2009, Martin *et al.* 2009, Ehrenfeld 2010). When plant invasion causes a decrease in soil pH, the solubility of phosphorous in soil is enhanced and high phosphorous availability often facilitates further invasion (Herr *et al.* 2007, Chen *et al.* 2009, Wang *et al.* 2015). The cation pools also show fluctuations (increase or decrease or in some cases, no change) in response to plant invasion, although these are largely dependent on field conditions (Ehrenfeld 2010).

A major reason for invasion success by means of chemical modification of the environment is allelopathy. Allelopathy could be defined as “any impact, direct or indirect, positive or negative (*e.g.*, phytotoxicity, soil sickness) of one organism on the growth and development of another organism through the release of chemical compounds into the environment” (Rice 1984, Elakovich & Wooten 1989; Cheng & Cheng 2015). Allelochemicals are usually released from roots, shoots, leaves or flowers which negatively affect the neighboring native species (Rice 1974). Allelopathy is a mechanism as suggested by ‘novel weapons’, where the invasive plant species negatively impacts native plant species which do not have tolerance or resistance to allelochemicals (Callaway & Ridenour 2004, Yadav *et al.* 2016). Allelopathy can affect the native plants directly by impacting germination and growth or indirectly by altering the environment which would in turn affect the native plant species (Cipollini *et al.* 2012). As allelopathy could alter the physiology of the species, it could alter the plant community structure (Rice 1992) which would in turn affect the litter and nutrient dynamics of the ecosystem. Allelopathy is a chemical means of interference competition where the basic nature of the substrates gets altered which affects the nutrient uptake of native plants and therefore the plant growth. The effects of allelochemicals are usually greater in the introduced range than the native range (Callaway *et al.* 2004, Inderjit *et al.* 2011, Gioria & Osborne 2014). Some studies have however reported that the secretion and release of allelochemicals as a means of resource competition may eventually reduce the growth of the same plant species and enhance their palatability to herbivores in the long run (Rasher & Hay 2014, Gioria & Osborne 2014).

The plant invasion thus causes serious deleterious impacts to the ecosystem by drastically altering the chemical properties and the effects may remain for a long time even after the invasive plant has been removed known as ‘soil-legacy effects’ (Jordan *et al.* 2011). Moreover, when the chemical exudates are leached from plants by rain or soil erosion, the chemical properties of soil at distant places away from the site of introduction are also invariably affected.

IMPACTS OF INVASION ON BIOLOGICAL ASPECTS

Invasive plants affect not only the abiotic components of the ecosystem, but also the biotic components. Invasive species affect the biological components of the ecosystem in various ways. The invasive plant species affect the species richness, evenness and abundance of the native plant species reducing the local species diversity and thereby drastically changing the unique characteristics of the original biological community present in the habitat (Olden & Poff 2003, Winter *et al.* 2009, Pyšek *et al.* 2012, Rastogi *et al.* 2015, Wekhanya 2016). Invasive plants have the ability to cause variations even at the level of genes of native populations by means of hybridization (Vilà *et al.* 2000, Pyšek *et al.* 2012). Invasive species may affect the species diversity and community structure by either exploitation competition (*e.g.* indirect interactions like resource-use) or by interference competition (*e.g.* direct interactions like allelopathy) or both (Callaway & Ridenour 2004, Charles & Dukes 2008). The impacts of invasive species via different kinds of interactions such as parasitism, predation, mutualism, herbivory, etc. can markedly alter the abundance of species, sometimes those with key traits that are essential to ecosystem functioning (Chapin *et al.* 2000, Charles & Dukes 2008). Invasive species also disrupt food chains, food webs by affecting energy flows and sometimes by eliminating keystone species (Dukes & Mooney 2004, Charles & Dukes 2008).

Not all the species that are introduced may thrive, although some may survive, become dominant and eventually replace the native species and become invasive. The native species diversity becomes dwindled or in some cases become locally extinct because they are unprepared to defend themselves from the invasiveness of the new species introduced. Invasive species alter the nutrient cycling and this may alter the microbial load as well as composition (van der Heijden *et al.* 2008). Overall, invasive plants pose various impacts on the native

biodiversity which could be summarized as follows: decrease in the diversity, density and abundance of the species (Kandwal *et al.* 2009); replacing the economically and ecologically important fodder grasses, medicinal plants, etc. (Bughani & Rajwar 2005); favouring the invasion of other alien species over the native endemic species (Dobhal *et al.* 2011); inhibiting the seed germination and growth of native flora (Bhardwaj *et al.* 2014); reducing the nutrient content of the soil by altering the soil physico-chemical properties (Bhatt *et al.* 1994) and homogenization of natural habitats (Dar & Reshi 2015, Pathak *et al.* 2019).

Invasive species alter the biological properties of the ecosystem via different methods. Apart from influencing the abiotic components and affecting the ecosystem processes, they are known to drastically alter the diversity and composition of both aboveground and belowground flora (Levine *et al.* 2003, Gaertner *et al.* 2009, Gioria *et al.* 2014, Gioria & Osborne 2014). Changes in the aboveground and belowground flora would also influence the nature of foliar herbivores as well as the natural enemies of these herbivores (Pineda *et al.* 2010, Soler *et al.* 2012, van der Putten *et al.* 2013). It would also in turn affect the diversity and composition of soil biota (van der Putten *et al.* 2013). The successful establishment of invasive species is mostly linked with better resource-use efficiency of the species that is attributed to its superior capacity to compete for various kinds of resources. Resource competition plays a major role in determining invasion success as it is involved in both naturalization and invasion phases (Beerling *et al.* 1994, Vilà & Weiner 2004, Gioria & Osborne 2014).

Water is a major resource for which the invasivespecies compete for in order to successfully establish themselves (Thebaud *et al.* 1996). Although native species are expected to succeed in the competition for water due to presumed adaptation strategies, invasive species prove to be better competitors in environments with water deficits (Nernberg & Dale 1997, Mason *et al.* 2012, Gioria & Osborne 2014). Another major resource the invasive species compete for is the light where the larger plant species obtain disproportionately large share of this resource, suppressing the smaller individuals (Keddy & Shipley 1989, Freckleton & Watkinson 2001). Invasive species usually have superior capacity to capture light energy due to larger sizes, higher specific leaf area, etc. than the native species and the subsequent shading caused hinders the native individuals (Hobbs & Mooney 1986, Hutchinson & Vankat 1997, Richardson *et al.* 2000, Kueffer *et al.* 2007, Iponga *et al.* 2008, Gioria & Osborne 2014). The reduction of light penetration at the ground level due to the establishment of invasive species often suppresses the growth of herbs. Although physical space is not a consumable resource, it is nevertheless an important factor for competition as it determines the access to other resources such as water, light and nutrients (McConaughay & Bazzaz 1991, Gioria & Osborne 2014). Phenology plays a crucial role in determining better utilization of resources. Early growth offers a competitive advantage to invasive species as it leads to early utilization of resources and avoid competition with the native species (Tiley *et al.* 1996, Wilsey *et al.* 2011, Wolkovich & Cleland 2011, Gioria & Osborne 2014). Invasive species experience not only interspecific competition with the native species, but also intraspecific competition with the neighbouring individuals (Weiner 1993, Suding & Goldberg 1999). The dominant species play a crucial role in determining the community structure of forest and other terrestrial ecosystems (Grime 1998, Smith *et al.* 2004). Both the dominant native species and the dominant invasive species compete for the same resources and increase their biomass (Grime 1998). Bottollier-Curtet *et al.* (2013) compared the dominant native and dominant alien invasive species and observed that dominant invasive species produced significantly greater aboveground and belowground biomass (Gioria & Osborne 2014).

The longer persistence of invasive species in a community than the native species could be owed to its phenotypic plasticity, which is the ability of a particular genotype to express a wide range of phenotypes in response to various environmental conditions. Phenotypic plasticity is often attributed to the enhancement of niche breadth (Bradshaw 1965, Richards *et al.* 2006). As invasive species possess high phenotypic plasticity in various morphological and eco-physiological traits, they out-compete most other species and successfully establish themselves (Gioria & Osborne 2014).The reason that could be attributed for successful establishment of invasive species is that they possess the ability to undergo rapid evolutionary changes in accordance with the novel environmental conditions in which they are introduced and hence adapt themselves quickly (Bossdorf *et al.* 2005). Apart from the diverse and direct competitions that the invasive species face, they also face indirect competitions such as the competition for pollinators. Invasive species are often known to disrupt the native plant-pollinator relationships as re-visitation to native species is reduced in the presence of invasive species (Brown *et al.* 2002, Muñoz & Cavieres 2008, Palladini & Maron 2013, Gioria & Osborne 2014).

Apart from influencing the native plant community structure and composition, invasive plants also cause changes in the soil microbial communities in such a way that it results in a positive feedback for the invasive plant species and a negative feedback for the native plant species (Callaway *et al.* 2004, Kulmatiski *et al.* 2008,

Callaway *et al.* 2008, TeBeest *et al.* 2009, Sanon *et al.* 2012, Si *et al.* 2013). As the litter quality gets varied with the prevalence of invasive plant species, the microbial community which decomposes the litter also gets altered (Wang *et al.* 2015). Moreover, as both invasive and native species occur in the same community, litter mixing occurs wherein the litter of invasive species is mixed with that of native species. Litter mixing brings about changes in resource quality and structure which therefore leads to changes in the microbial community composition (Chen *et al.* 2013, Zhang *et al.* 2014, Wang *et al.* 2015). The bacteria are known to dominate in early succession which is gradually replaced by fungi in late succession (Jiang *et al.* 2009, Si *et al.* 2013). In many cases, fungi are known to dominate the low-quality litters as they have lower nutrient requirements than the bacteria (Wang *et al.* 2011, Wang *et al.* 2015). This is so because in general, fungi have a greater carbon:nitrogen ratio than bacteria, which therefore has lesser nutrient requirements. Given that the access to carbon is equal but nitrogen is limited, then the microbial community shifts towards fungal dominance. On the other hand, if there is no limitation of nitrogen, then the microbial community shifts towards bacterial dominance (Simba *et al.* 2013, Wekhanya 2016).

When the soil microbial community composition gets altered with invasive plants, their ecosystem functions also change from that of original microbial community, which would in turn impede with ecosystem processes (Ehrenfeld 2003). Invasive plants therefore interfere with the co-operation existing between the soil microbes/networks and the native plants which would in turn facilitate invasion success (Reinhart & Callaway 2006, Dawson & Schrama 2016, Ricciardi *et al.* 2017). The introduction of invasive plants in a healthy ecosystem often disturbs the mutualistic relationships between fungi and the native plants, especially mycorrhizal associations. Invasive plant species usually disrupt such mutualistic relationships either by modifying soil food webs or by altering the soil nutrient dynamics or by instigating pathogens (Ehrenfeld *et al.* 2005). Therefore, soil microbes are often considered to be one of the key factors that either encourage or suppress plant invasions (van der Putten *et al.* 2013, Inderjit & Cahill 2015).

Soil microbial community plays a critical role in litter decomposition and nutrient cycling through the action of soil enzymes. The most important soil enzymes are β -glucosidases, proteases, ureases and phosphatases which are involved in carbon, nitrogen and phosphorous cycles (Sardans & Penuelas 2005, Sardans *et al.* 2008). The action of soil enzymes is dependent on soil microbial networks (Allison & Vitousek 2004). When invasive plants take over a new habitat, the soil networks are disrupted leading to the interference in the activity of these important enzymes that are responsible for soil fertility and soil maintenance (Aon & Colaneri 2001, Flory & Clay 2010).

Plant invasions not only affect the native plants and soil microbial community, but they also affect soil fauna. Plant invasion affects soil micro-fauna as well as invertebrates inhabiting both aboveground and belowground (Kourtev *et al.* 2003, Qin *et al.* 2019). Invertebrates play an important role in the decomposition of organic matter as they quicken the decomposition of litter and nutrient release, especially in tropical forests (Schadler & Brandl 2005, Lavelle *et al.* 2006, Meyer *et al.* 2011). However, the decomposition activity of invertebrates largely depends on litter chemistry and also the decomposer network (Powers *et al.* 2009). The introduction of alien invasive species in an ecosystem is found to decrease the species richness and diversity of the native invertebrate fauna. However, the impacts of plant invasion on invertebrate fauna may vary depending on the invasive species involved as some plant invasions favour certain kinds of invertebrate fauna and eliminate other taxa (McGrath & Binkley 2009, Qin *et al.* 2019).

Changes in plant community structure arising due to plant invasion have proven to be detrimental to arthropods because many arthropods require specific plants for food and reproduction (Litt *et al.* 2014). The novel plants introduced may not be recognized by native arthropods leading to reduction in the latter's abundance and diversity (Tallamy 2004). Moreover, changes in the stand structure caused due to plant invasions may restrict arthropod movement, distribution and therefore reproduction by modifying the environmental conditions such as light, temperature, moisture, etc. (Wolkovich *et al.* 2009, Talley *et al.* 2012, Litt *et al.* 2014). The alteration in soil physico-chemical properties such as soil pH, soil salinity, soil nutrient availability, soil moisture, etc. due to plant invasions may affect the diversity and reproduction of belowground-dwelling arthropods (Gratton & Denno 2005). The changes in arthropod composition and distribution would also inflict changes in the predator composition and distribution (Pearson 2009, Litt *et al.* 2014). Among the various functional groups affected by plant invasion, only the detritivores are likely to benefit due to the plentiful availability of food and favourable microclimatic conditions (Levin *et al.* 2006). As per Standish (2004), the rate of litter decomposition is higher in invaded areas than in non-invaded areas, which indicates the abundance of detritivores in invaded areas. Such an ecosystem-wide abundance and distribution of detritivores would lead to

ecosystem-wide shifts in trophic dynamics – from feeding on live vegetation to feeding on detritus (Gratton & Denno 2006, Levin *et al.* 2006, Litt *et al.* 2014). Thus, plant invasions greatly affect the biological aspects of ecosystems.

CONCLUSION

Thus, it becomes evident from the review that plant invasions are a global concern that impact the physical, chemical and biological aspects of the ecosystems. The impacts of the plant invasions may vary according to the spatio-temporal context as well as the idiosyncratic properties of the invasive species. Due to increased globalization, there is a great chance for both unintentional/intentional introductions of species into new environments. Moreover, invasive species are well-known to expand their ranges towards high latitudes and altitudes due to climate change and exacerbated by anthropogenic disturbances. Therefore, more stringent screening and monitoring methods have to be adopted to check undesirable introductions. Based on the available data repositories, the species related to the already known invasive species should be screened for traits of invasiveness. In the case of infested ecosystems, the functional trait-based approach, *viz.* early detection and rapid response, eradication, mitigation and restoration should be used to restore ecosystems. A better understanding on the impacts of biological invasion on biogeochemistry of forest ecosystems, long-term monitoring is needed for developing proper management strategies to combat plant invasions.

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