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Article

What makes the plant invasion possible? Paradigm of invasion mechanisms, theories and attributes

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Abstract

Plant invasion is the second most severe threat to biodiversity after habitat fragmentation. Invasive species are alien species whose introduction and spread threatens ecosystems, habitats or species with socio-cultural, economic and/or environmental harm, and harm to human health. Present review precisely describes the global problems of invasion in different ecosystems, continents and its multifaceted impacts. Plant invasion is now increasingly being recognized as global problem and various continents are adversely affected, although to a differential scale. Quest for the ecological mechanism lying behind the success of invasive species over native species has drawn the attention of researches worldwide particularly in context of diversity-stability relationship. Transport, colonization, establishment and landscape spread may be different steps in success of invasive plants and each and every step is checked through several ecological attributes. Further, several ecological attribute and hypothesis (enemy release, novel weapon, empty niche, evolution of increased competitive ability etc.) were proposed pertaining to success of invasive plant species. However, single theory will not be able to account for invasion success among all environments as it may vary spatially and temporally. Therefore, in order to formulate a sustainable management plan for invasive plants, it is necessary to develop a synoptic view of the dynamic processes involved in the invasion process. Moreover, invasive species can act synergistically with other elements of global change, including land-use change, climate change, increased concentrations of atmospheric carbon dioxide and nitrogen deposition. Henceforth, a unified framework for biological invasions that reconciles and integrates the key features of the most commonly used invasion frame-works into a single conceptual model that can be applied to all human-mediated invasions.

Keywords invasion; phenotypic; productivity; disturbance.

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1 Introduction

As a result of the rapid land use changes, the pace of invasion has particularly accelerated during the past century (Schei, 1996; Sharma et al,. 2005; Zhang and Chen, 2011; Rai, 2013; Briggs, 2013, 2014). However, invasive plants are actually like native plants, not bad by birth, is just a matter of being in a favourable environment or possessing certain ecological attributes which triggers them as invasive ones. It is rather impossible to predict the ecological behaviour of a species in a new environment (Anon, 1998; Williamson, 1999; Lüi, 2011; Priyanka et al., 2013). Species whose native status and origin are not clear is called cryptogenic species (Carlton, 1996; Sharma et al., 2005).

Quest for the ecological mechanism lying behind the success of invasive species over native species has drawn the attention of researches worldwide (Keane and Crawley, 2002; Totland et al., 2005; Rai, 2013). In this regard, ecologists are trying to investigate the prime factors that determine plant abundance (Van der Putten, 2002; Rai, 2013).

Transport, colonization, establishment and landscape spread may be different steps in success of invasive plants and each and every step is checked through several ecological attributes (Fig. 1). Transport of invasive plants in the form of seed/seedlings is checked through propagule pressure necessary for colonization which in turn is checked by different abiotic factors (like temperature, sunlight, moisture etc.). Lockwood et al., (2005) reviewed that propagule pressure is a key element to understanding why some introduced populations fail to establish whereas others succeed. Even if the exotic plants are able to colonize, native plants offer biotic resistance for their establishment. After escaping biotic resistance, invasive plants spread rapidly across the landscape. Landscape spread is also constrained through habitat connectivity and dispersal ability. Moreover, all these steps are inextricably linked with global environmental change, fire/disturbance regime and extinction of native biodiversity through land use change or habitat fragmentation (Fig. 1).

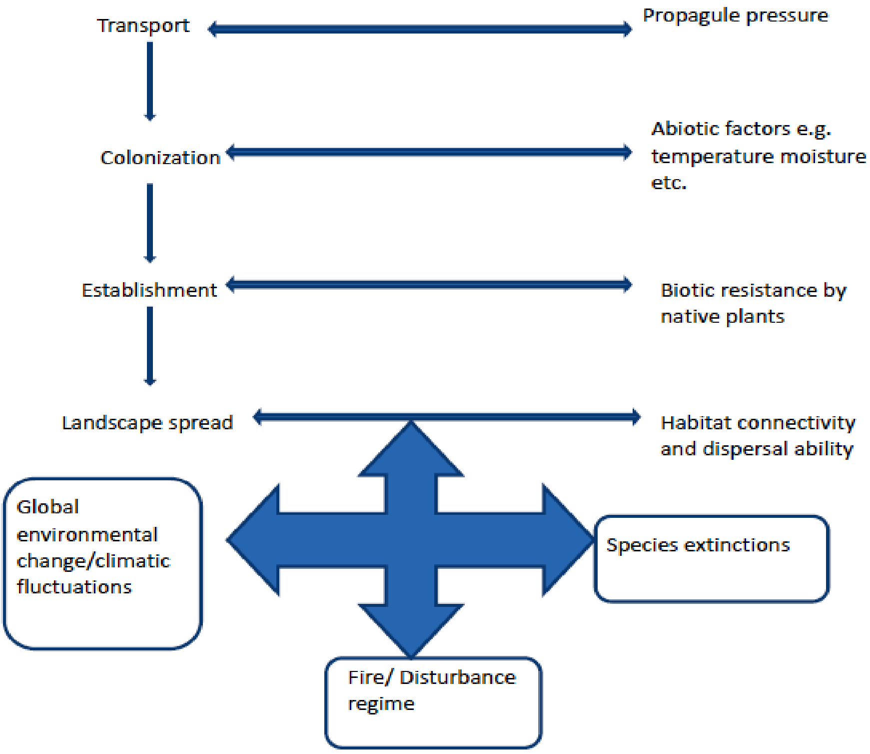

Fig. 1 Filters or checkpoints and factors affecting different steps of invasion (Modified after Chapin et al., 2002; Theoharides and Dukes, 2007; Rai, 2013).

Davis et al. (2000) opined that the elusive nature of the invasion process arises from the fact that it depends upon conditions of resource enrichment or release that have a variety of causes but which occur only intermittently and, to result in invasion, must coincide with availability of invading propagules. The actual invasion of an environment by new species is influenced by three factors, i.e., the number of propagules entering the new environment (propagule pressure), the characteristics of the new species, and the susceptibility of the environment to invasion by new species (invasibility) including the region's climate, the environment's disturbance regime, and the competitive abilities of the resident species (Lonsdale, 1999; Davis et al., 2000; Rai, 2013).

To understand the factors that determine plant invasiveness and competitive ability (Field et al., 2006) is a major challenge in plant biology. The threat posed by non-native invasive plant species has spurred efforts to identify individual species that show a high probability for naturalization and/or invasiveness and to rapidly eradicate those species while their distributions are limited or prevent their introduction. However, there is a widespread perception that predictions about which species will invade are impossible (Enserink, 1999). Colautti and MacIsaac (2004) synthesized an invasional framework based on current models that break the invasion process into a series of consecutive, obligatory stages. Under their framework, invasions can be more objectively understood as biogeographical, rather than taxonomic, phenomena (Colautti and MacIsaac, 2004; Rai, 2013).

In order to define the plant-environment interaction, it is useful to consider the environment as a series of filters which prevent unsuited plants from establishing, maturing, reproducing and dispersing (Keddy, 1992; Rai, 2013). The selection of the appropriate autecological attributes and environmental filters requires an understanding of how the system functions. (Higgins and Richardson, 1996). Both the biotic and abiotic properties of the target habitat are likely to be as important as the aut-ecological attributes of the invading species in influencing invasive success (Higgins and Richardson, 1996; Rai, 2013).

Inextricable linkage and interactions between climate change, species invasions, and habitat fragmentation could cause further diversity losses, because many species may be unable to migrate through fragmented habitats to reach regions with suitable climates and soils (Sala et al., 2000; Tilman et al., 2001; Crossman et al., 2011; Rai, 2013).

1.1 Invasion window

The *"invasion window"* concept (Johnstone, 1986; Rai, 2013) emphasizes the importance of the temporal availability of resources in influencing invasive success. Equally important, however, is the spatial pattern of resource availability. Resources in terms of resource availability and disturbance play an important role in the process of plant invasion. Resource availability includes factors such as nutrient, moisture and space availability which can be regarded as manifestations of spatial and temporal environmental heterogeneity. The importance of environmental heterogeneity in influencing invasion patterns is well established. For example, Lonsdale (1993) observed a strong correlation between the areal spread of the invasive shrub *Mimosa pigra* in a tropical wetland of northern Australia and the previous year's rainfall. Similarly, Williams et al. (1987) noted that establishment of *Baccharis pilularis* ssp. *consanguinea* in northern California grassland was correlated with annual and spring rainfall. In another example, nutrient availability strongly influenced the invisibility of Californian serpentine grassland by alien annual grasses (Hobbs et al., 1988; Huenneke et al., 1990). Both biotic and abiotic attributes of the environment were experimentally shown to govern the invasibility of a Californian coastal plant community (D'Antonio, 1993; Rai, 2013). The same was illustrated more indirectly in a multiple regression analysis which related a number of habitat and land-use attributes to the distribution and spread of the invasive shrub *Rhododendron ponticum* in North Wales (Thomson et al., 1993; Rai, 2013).

1.2 Phenotypic plasticity

In plants, the well developed plasticity of many traits is usually interpreted as an adaptive response to environmental heterogeneity as a consequence of immobility and modular growth (Dorken and Barrett, 2004; Rai, 2013). Although studies of phenotypic plasticity have a long history in plant ecology (Bradshaw, 1965; Schlichting, 1986; Scheiner, 1993; Schlichting and Pigliucci, 1998; Dorken and Barrett, 2004; Rai, 2013), the extent to which patterns of plasticity differ among traits, life histories and habitats, and the adaptive basis of this variation are largely unresolved questions.

In the C_4 African grass, *Pennisetum setaceum*, on the other hand, phenotypic plasticity was more important than local adaptation to dominance across diverse habitats on Hawaii (Kollmann and Bañuelos, 2004); similar results were reported for the invasive alien *Agrostis capillaries* in New Zealand (Rapson and Wilson, 1992; Kollmann and Bañuelos, 2004).

Dorken and Barrett (2004) investigated the plasticity of vegetative and reproductive traits in *Sagittaria latifolia*, a clonal aquatic plant whose populations are both monoecious and dioecious. They (Dorken and Barrett, 2004) evaluated the prediction that populations of the two sexual systems would have different patterns of phenotypic plasticity because of the contrasting habitats in which they occur and found significant plasticity for female sex allocation in monoecious populations, with more female flowers at higher nutrient levels. Järemo and Bengtsson (2011) shows that the organism life-history may control the effect of age of introduced individuals on the probability of establishment of a new population and that competition has a larger effect on semelparous organisms than iteroparous. Therefore, life history traits and age structure may also play an important role in invasion process (Järemo and Bengtsson, 2011).

Kollmann and Bañuelos (2004) described variations in growth and phenology in 26 populations of *Impatiens glandulifera* from nine European regions in a common garden in Denmark. They (Kollmann and Bañuelos, 2004) described the potential consequences of such latitudinal trends for population dynamics and dispersal of alien plants. Small colonizing populations generally have increased rates of evolution, and that might be particularly true in invasive alien species (Eckert et al., 1996; Lee, 2002; Kollmann and Bañuelos, 2004; Rai, 2013). One other example is the European grass *Bromus tectorum* which shows local adaptations along an environmental gradient from arid steppe vegetation to subalpine forests in western North America (Rice and Mack, 1991; Kollmann and Bañuelos, 2004).

1.3 Disturbance

Disturbance plays a prime role in invasion ecology. Disturbances can be defined as resource fluctuations which are discrete relative to the temporal scale of investigation (White and Pickett, 1985; Rai, 2013). There is an array of research works on varying ecosystems which studied the impacts of several disturbances on the success of invasive species and experimental studies have illustrated the role of disturbance in an invasion context. Disturbance may be in the form of fire as observed in South African fynbos which creates the space and provide an opportunity so that alien trees can establish themselves (Richardson and Cowling, 1992; Rai, 2013). Further, Fox and Fox (1986) concluded that "there is no invasion of natural communities without disturbance". Although anthropogenically modified disturbance regimes have, in particular, been implicated as invasion facilitators (Fox and Fox, 1986; Hobbs and Huenneke, 1992), invasions can occur under a natural disturbance regime (Richardson et al., 1992). Long term impacts of forest harvesting may result in invasion of exotic plant species (Marshall, 2000). Intensive grazing in forest ecosystems may exacerbate the alien problem particularly after fire (Keeley, 2004; Rai, 2013).

Hobbs (1989) showed that the presence of disturbed areas can enhance the establishment rate of invasive plants. Similarly, Bergelson et al., (1993) found that the area and spatial distribution of disturbed areas influenced invasive plant spread. Invasion case studies, through the use of correlative evidence have, like the experimental studies, also implicated disturbance. For example, DeFarrari and Naiman (1994) concluded from an alien plant survey that disturbance type and time since disturbance were the major factors influencing invasibility in Washington, USA. In another survey 90% of the alien species on Lord Howe Island, Australia, were associated with disturbed areas (Pickard, 1984). Similarly, the analysis by Crawley (1987) of floristic data of the British Isles revealed that aliens constituted more than 50% of the flora in highly disturbed areas, but less than 5% of the native woodland flora. MacDougall et al., (2006) found that low-stress environments were less invasible but appear to be more susceptible to invasion by species with strong competitive impacts.

Almost all this effort has been expended on observations of invasions in natural systems (de Waal et al., 1994; Pysek et al., 1995; Brock et al., 1997; Rai, 2013). There have been few attempts to study invasion experimentally, by manipulating either the characteristics of the invaded community or the identity of potential invaders (Peart and Foin, 1985; Robinson et al., 1995; Bastl et al., 1997; Tilman, 1997; Crawley et al., 1999; Knops et al., 1999; Levine, 2000; Thompson et al., 2001). Thompson et al. (2001) examined the roles of productivity and disturbance as major factors controlling the invasibility of plant communities, and simultaneously through field experiments identified the functional characteristics of successful invaders in response to different types of invasion opportunity. Field experiments established in 1990 comprised of seeds of 54 native species, not originally present at the site, were sown into fertility X disturbance matrix established in unproductive limestone grassland at the Buxton Climate Change Impacts Laboratory (BCCIL). Thompson et al. (2001) results were consistent with the hypothesis that invasions are promoted by an increase in the availability of resources, either through addition of extra resources or a reduction in their use by the resident vegetation. Volin et al. (2004) opined that invasion success of *Lygodium microphyllum* in disturbed as well as undisturbed greater Everglades ecosystem of southern Florida, USA may be attributed to the traits related to its reproduction, such as propagule pressure, and its ability to grow in a lowlight understorey environment. Maestre (2004) in his study in SE Spain along a disturbance gradient predicted that patch attributes are the major determinants of species richness and diversity in semiarid *Stipa tenacissima* steppes. Population and soil seed bank dynamics of *Nicotiana glauca* demonstrated that Disturbances in plant communities provide opportunities for weed germination, propagation, spread, and invasion (Florentine et al., 2006). Different invasive plants may evolve certain adaptable strategies in order to cope up with the disturbances e.g. accumulation of dormant but long-lived viable seed reserves serve as sources of regeneration of new *Prosopis juliflora* plants in the event of disturbance that might eliminate the aboveground stands (Shiferaw et al., 2004).

Leaf traits (specific leaf area (SLA), foliar nitrogen and phosphorus; N:P ratio) comparisons between natives and exotics at disturbed as well as undisturbed sites were significantly higher for exotics at disturbed sites compared with natives at undisturbed sites, with natives at disturbed sites being intermediate. Therefore, species with leaf traits enabling rapid growth will be successful invaders when introduced to novel environments (Leishman et al., 2007).

The role of road corridors in landscape fragmentation and disturbance, and as a reservoir of non-native plant species is scanty in literature (Angold, 1997; Forman and Alexander, 1998; Forman and Deblinger, 2000;

Saunders et al., 2002; Gelbard and Belnap, 2003; Godefroid Koedam 2004). The altered disturbance regime in plant communities along corridor edges and vehicle traffic facilitate the spread and establishment of invasive non-native plant species (Hansen and Clevenger, 2005). Hansen and Clevenger (2005) compared the frequency of non-native plant species along highways and railways and the ability of these species to invade grasslands and dense forests along these corridors and emphasized the importance of minimizing the disturbance of adjacent plant communities along highways and railways during construction and maintenance, particularly in grassland habitats and in areas sensitive to additional fragmentation and habitat loss.

2 Theories/Hypotheses/Factors for Invasion

Several theories have been proposed pertaining to ecological attributes or mechanisms responsible for invasion (Fig. 2). Ultimately, it is unlikely that any single theory will be able to account for all differences in invasibility among all environments (Davis et al., 2000). A plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources (Davis et al., 2000). In his recent article in *Nature*, Seastedt (2009) indirectly supported 'resource and enemy release hypothesis' (R-ERH), given by Blumenthal (2006). He opined that resource fluctuations and lack of enemies (fungal and viral pathogens) may act in concert, underpinning for invasion success. However, these two factors, instead of acting as drivers, merely act as passengers along for the invasion ride. Nevertheless, there exists a cascade of mechanisms behind the invasion success.

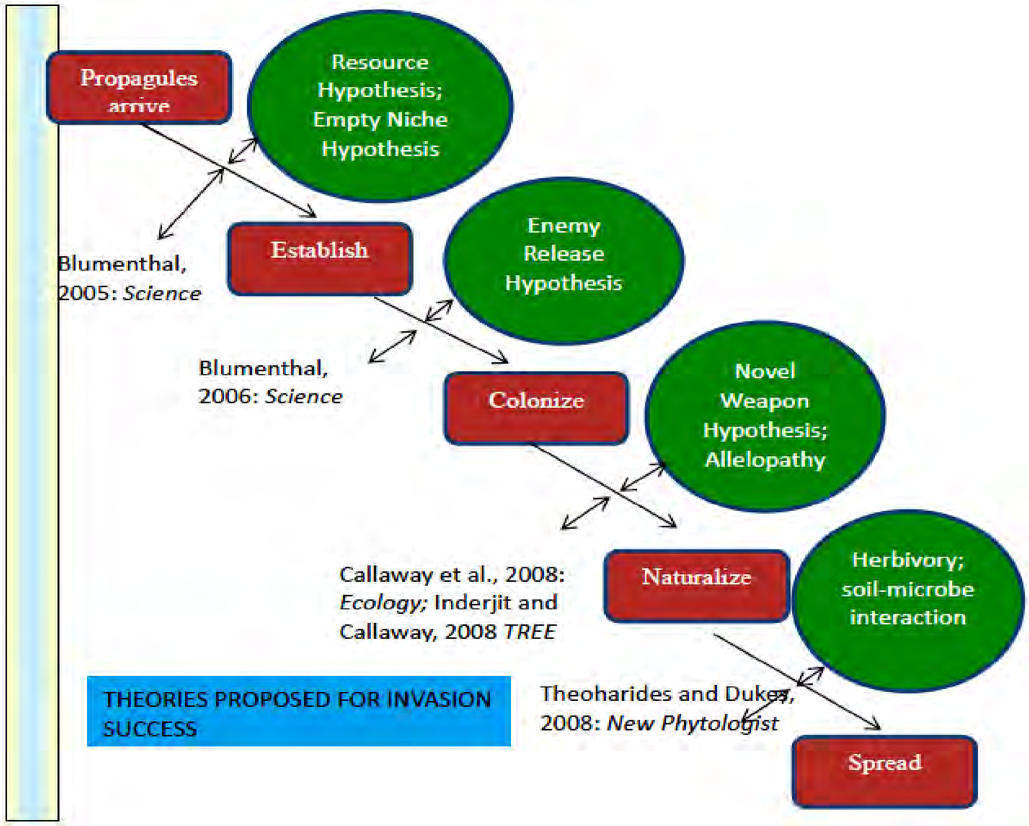

Fig. 2 Salient hypothesis/theories applicable at varying invasion stages (After Rai, 2013).

2.1 Enemy Release Hypothesis

Enemy release hypothesis reveals that if an organism introduced into a new region leaves behind its natural predators, competitors, and parasites, its chances of reproductive success increase. Competition for mutualistic interactors among exotic and native plant species provides another angle to the enemy release hypothesis (Keane and Crawley, 2002). Complete understanding of the role of enemy release in exotic plant invasions is prerequisite in order to prepare a comprehensive predictive model of exotic plant invasions (Keane and Crawley, 2002).

However, it is worth to mention that two of the most well known and best studied are the enemy release hypothesis (ERH) (Elton, 1958; Keane and Crawley, 2002; Blumenthal 2005, 2006; Rai, 2013) and the resource hypothesis (Davis et al., 2000; Blumenthal et al., 2003; Blumenthal, 2005, 2006) and both are ecologically interrelated (Blumenthal, 2005, 2006. Blumenthal (2005, 2006) emphasized that plant invasions is likely to involve not only multiple mechanisms of invasion (resource–enemy release hypothesis), but also understanding the conditions under which each mechanism tends to be important i.e. the effects of enemy release may be strongest for high-resource species. Increasing realization of aforesaid mechanisms may assist in the management of invasive species (Blumenthal, 2005, 2006). *Mikania micrantha* (mile a minute weed) is one of the top 10 worst weeds in the world (Tab. 1) mainly because of lack of natural enemies, a wide range of invasive habitats, and increased human disturbance associated with recent economic growth (Zhang et al., 2004).

2.2 Novel Weapon Hypothesis (NWH)

The novel weapons hypothesis raises the possibility of co-evolution among plants in different regions of the Earth, and that mixing species from different regions increases the chances of disrupting the ecological processes that lead to species coexistence and greater community diversity (Callaway and Ridenour, 2004; Vivanco et al., 2004; Rai, 2013). *Centaurea maculosa* (spotted knapweed), an invasive species in the western United States, displaces native plant species by exuding the phytotoxin (–)-catechin from its roots (Bais et al., 2003). Bais et al. (2003) demonstrated the allelopathic effects of *C. maculosa* by integrating ecological, physiological, biochemical, cellular, and genomic approaches and their results supported a “novel weapons hypothesis” (NWH) (Callaway and Aschehoug 2000, Callaway and Ridenour, 2004; Vivanco et al., 2004) for invasive success.

2.3 Resource (R)/nutrients

One mechanism by which high resource availability might increase invasibility is by increasing the ability of non-native plants to compete with natives. Nutrients addition to soils (e.g. Wedin and Tilman, 1996; Bakker and Berendse, 1999; Kolb et al., 2002; Rai, 2013) as well as water (Milchunas and Lauenroth, 1995; White et al., 1997; Kolb et al., 2002) promotes invasion. Sharma and Raghubanshi (2009) studied impact of *Lantana camara* vegetative understory invasions on soil nitrogen (N) availability in forest ecosystems (Vindhyan forests, India) and observed alteration in litter inputs and chemistry beneath the lantana canopy positively and significantly altered soil N availability, N-mineralization, and total soil N. Another study (Osunkoya and Perrett, 2011) demonstrated that under *Lantana* infested soil, moisture, pH, Ca, total and organic C, and total N were significantly elevated, while sodium, chloride, copper, iron, sulfur, and manganese, many of which can be toxic to plant growth if present in excess levels, were present at lower levels in soils compared to soils lacking *L. camara*. Likewise, garden and greenhouse experiments have shown that high nutrient or water availability can increase the ability of non-native plant species to compete with natives (Wedin and Tilman, 1993; Nernberg and Dale, 1997; Claassen and Marler, 1998; Kolb et al., 2002). In most cases, it has been demonstrated that the native species outperformed the alien under conditions of reduced light, nutrient or water availability (Daehler, 2003; Totland et al., 2005).

In mediterranean coastal dune ecosystem, long-term invasion by *Acacia longifolia* altered the soil properties with increased levels of organic C, total N and exchangeable cations resulting in higher microbial biomass, basal respiration, and b-glucosaminidase activity (Marchante et al., 2008). Further, Siemann et al. (2007) observed the impact of nutrient loading and extreme rainfall events on coastal tallgrass prairies found that it was more likely to be impacted by nutrient loading, in terms of invasion intensity. It has been demonstrated that microbial biomass C, N, and P all increased as the cover of *M. micrantha* increased, therefore, we can say that its invasion improved the soil attributes which in turn lead to its greater invasive success (Li et al., 2007).

Invasive plants may inhibit N-fixation and possibly lead to long-term declines in N inputs to soil (Wardle et al., 1994). The complex interactive effects of invasion on soil N-cycling are illustrated by grass invasion into submontane woodlands in Hawaii in which the grass increased net mineralization in the wet season due to changes in soil organic matter, but decreased net mineralization in the dry season due to decreases in soil moisture (Mack and D’Antonio, 2003; Bohlen, 2006). Morghan and Seastedt (1999) in their study on non-native plants, e.g., *Centaurea diffusa* and *Agropyron smithii* found that carbon amendment treatment (with sugar and sawdust) alone is not sufficient in order to sites deeply infested by invasive species.

Frequent small- scale disturbances, e.g. by burrowing animals, can create localized patches of unexploited resources, and thereby may facilitate invasions (Hobbs and Mooney, 1985; Davis et al., 2000). Nitrogen addition in California serpentine grassland increased the invasion success of several alien grass species (Huenneke et al., 1990) and Harrison (1999) argued that the low invasibility of serpentine grasslands was due to low levels of soil nutrients. Maron and Connors (1996) concluded that invasions by exotic species in a California coastal prairie were facilitated by a native nitrogen-fixing shrub. Similar findings were found by Hobbs and Atkins (1988) who also found that disturbance combined with Eutrophication increased a community's invasibility. The combination of disturbance and eutrophication involves both a reduction in resource uptake by resident vegetation and an increase in gross resource supply.

Likewise, other studies (Burgess et al., 1991; Harrington, 1991; Hobbs and Mooney, 1991; Li and Wilson, 1998; Davis et al., 1999; Dukes and Mooney, 1999; Rai, 2013) have shown that in dry regions, increase of water supply increases the invasibility of vegetation, either as a direct effect of water supply or through improved access to mineral nutrients. Imposed drought conditions reduced the availability of soil water and hence decreased the invasibility of the same communities during the drought period (Davis et al., 1998, Davis et al., 1999). Some authors have predicted that the increase in atmospheric CO_2 will favour invasions by certain species by increasing soil water availability due to more efficient use of water by the resident plants (Idso, 1992; Johnson et al., 1993; Dukes and Mooney, 1999; Davis et al., 2000; Rai, 2013). This is an example of increased resource availability due to reduced uptake by the resident vegetation. Others have argued that invasions may be facilitated by increases in precipitation (Dukes and Mooney, 1999; Rai, 2013), an example of increased resource availability due to increased resource supply. Still others have argued that the global nitrogen In aquatic ecosystems, eutrophication resulting from anthropogenic activities is already facilitating invasions (Wedin and Tilman, 1996; Rai, 2013), another example of enhanced supply increasing resource availability.

Brooks (2003) showed that the negative impact of N addition and enhanced growth of nonnatives on native annuals in the Mojave desert only occurred in the year of highest abundance of annual plants, which in turn was regulated by winter rainfall.

Whether alien or native, species cannot maximize growth, reproduction and competitive ability across all environments. So the success of invasive species is habitat-dependent (Funk and Vitousek, 2007; Rai, 2013). The interaction between habitat traits and intraspecific variation are found to be important when determining invasion success as experimented in case of invasive weed mugwort, *Artemisia vulgaris* (Barney et al., 2005). General assumption that invasive species colonize resource rich environment was contradicted by Funk and Vitousek (2007) who emphasized that invaders do colonize resource-poor environments and traits associated with resource conservation are widespread among species adapted to resource-poor environments employing resource conservation traits such as high resource-use efficiency.

2.4 Niche opportunities/ Presence of empty niches

Community ecology theory can be used to understand plant invasions by applying recent niche concepts to alien species and the communities that they invade (Shea and Chesson, 2002; Rai, 2013). These ideas lead to the concept of ‘niche opportunity’, which defined conditions that promote invasions in terms of resources, natural enemies, the physical environment, interactions between these factors, and the manner in which they vary in time and space (Shea and Chesson, 2002; Rai, 2013). Recent niche theory clarifies the prediction that low niche opportunities/invasion resistance result from high species diversity. Conflicting empirical patterns of invasion resistance are potentially explained by co-varying external factors. These various ideas derived from community ecology provide a predictive framework for invasion ecology (Shea and Chesson, 2002; Rai, 2013).

Invasion success also relies on suitability of niche dimension (Badano and Pugnaire, 2004). In this context, *Agave* species in Spain can be cited which showed higher rhizome and bulbil production, and higher establishment rates by agaves in sandy soils than in clay soils (Badano and Pugnaire, 2004). This suggested that sandy soils provide an opportunity which releases the clonal reproduction of *Agave*. Furthermore, the effects of agaves on the physiological performance and reproduction of native species were negative, positive or neutral, depending on the size and rooting depth of neighbours (Badano and Pugnaire, 2004).

2.5 Allelopathic Advantage against Resident Species (AARS)

A logical extension of the NWH is the hypothesis that populations of invaders in the invaded region should evolve greater concentrations of allelopathic, defense or antibiotic biochemicals than populations of the species in their native range (Inderjit et al., 2006; Rai, 2013). This hypothesis has been called the ‘allelopathic advantage against resident species’ (AARS). If invaders possess allelochemical weapons that provide greater competitive advantages in their new habitats than in their original ranges, then selection may act directly on those traits (Callaway and Ridenour, 2004). The fundamental prediction of AARS is that invasive populations will be more allelopathic, or better biochemically defended, than source populations (Callaway and Ridenour, 2004**;** Inderjit et al., 2005, Inderjit et al., 2006). Allelopathic effects not only derive from the release of phytotoxins from roots, but also from biochemicals present in leaves that leach during rainfall or release chemicals after senescing and falling to the ground (Inderjit and Keating 1999; Inderjit et al., 2006). Plant invasion is a huge and complex area that encompasses many aspects in addition to the potential contribution of Allelochemicals (Field et al., 2006). Allelopathy is one such mechanism that has been implicated in the success of at least some of the best known plant invaders in the world (Weir et al., 2004; Allaie et al., 2006), including *Eltrygia repens* (Weston et al., 1987; Korhammer and Haslinger, 1994; Allaie et al., 2006), *Bromus* *tectorum* (Rice 1974; Allaie et al., 2006), *Circium arvense* (Stachon and Zimdahl, 1980; Allaie et al., 2006), *Cyperus rotundus* (Agarwal et al., 2002), *Eichhornia crassipes* (Gopal and Sharma, 1981; Allaie et al., 2006), *Lantana camara* (Saxena, 2000; Allaie et al., 2006; Rai, 2013), *Parthenium hysterophorus* (Kanchan and Jayachandra, 1980; Kohli and Batish, 1994; Pandey, 1994; Tefera, 2002; Singh et al., 2003; Allaie et al., 2006; Rai, 2013) and *Prosopis* spp. (Goel et al., 1989). The most credible evidence for the involvement of allelopathy in plant invasion has come from the study of Bais et al. (2003) and Callaway and Aschehoug (2000) on *Centaurea* species in North America. Several biochemical and physiological processes of the susceptible species are affected by the allelochemicals released by such invasive species in their environment (Weir et al., 2004). Invasive species like *Eupatorium adenophorum*, dominant in some part of North East India is shown to exhibit allelopathic impact (Tripathi et al., 1981). In riparian habitats Reinhart et al. (2005) demonstrated that *Acer platanoides* trees suppress most native species, including the regeneration of the natural canopy dominants, but facilitate conspecifics in their understories.

Several arguments on allelopathy lead to the hypothesis that plant species that normally coexist should evolve resistance to each others' toxins, but not to the toxins of species with which they do not coexist i.e. invasive species (Fitter, 2003). The observation by Bais et al. (2003) on *C. maculosa* provided strong evidence for the differential susceptibility of target plants to a phytotoxin ((−)-catechin), and supports the discovery of an ecologically important allelopathic interaction. The toxin promotes production of reactive oxygen species in the roots of susceptible plants, which activates a Ca^{2+}-signaling cascade that initiates extensive changes in gene expression and death of the root system (Bais et al., 2003). Leaf leachate of *Anthemis cotula* inhibits seed germination of the commonly cultivated field crops in Kashmir valley (Allaie et al., 2006).

2.6 Biochemical basis of invasion

Biochemical basis is an extension or explanation for AARS as mentioned earlier. The invading species produces a phytotoxin, catechin, which induces oxidative stress in many native plants and often thereby eliminates them entirely from the local ecological community (Inderjit et al., 2006). Further, the findings of Inderjit et al., (2006) highlighted the role for the biochemical potential of the plant as an important determinant of invasive success besides earlier existing enemy release hypothesis (Kennedy et al., 2002) pointing that invasiveness is mainly due to enhanced resource competition after escape from natural enemies. *Cyperus rotundus* (nutgrass) is the world's worst invasive weed through tubers since its extract inhibits acetylcholinesterase activity from animal and plants as well as inhibits germination and seedling growth in wheat and tomato (Sharma and Gupta, 2007). Apart from case study on *Centaurea* sp., root exudates from *Acroptilon repens* (Russian knapweed) were found to be phytotoxic and the phytotoxin in the exudate was identified as 7,8-benzoflavone (a-naphthoflavone) (Stermitz et al., 2003; Rai, 2013).

Many invasive weeds, however, eventually encounter their native, coevolved enemies in areas of introduction (Zangerl and Berenbaum, 2005; Zangerl et al., 2008). Examination of herbarium specimens of an invasive phytotoxic European weed, *Pastinaca sativa*, through 152 years reveals phytochemical shifts coincident in time with the accidental introduction of a major herbivore, the parsnip webworm, *Depressaria pastinacella* (Zangerl and Berenbaum, 2005; Zangerl et al., 2008). In the aforesaid reassociation with a coevolved specialist in invaded area profoundly altered the selection regime, favouring trait remixing and rapid chemical changes in parsnip populations, as predicted by the geographic mosaic theory (Zangerl et al., 2008). That uninfested populations of New Zealand parsnips contain higher amounts of octyl acetate, a floral volatile used by webworms for orientation, suggests that plants that escape from specialized enemies may also experience selection to increase kairomones, as well as to reduce allomones (Zangerl et al., 2008).

2.7 Evolution of Increased Competitive Ability (EICA)

Among the more specific hypotheses considered was the evolution of increased competitive ability (EICA) of plants in the absence of specific herbivores (Bais et al., 2003; Rai, 2013). The EICA hypothesis predicts that once an organism escapes its natural enemies, it no longer needs the defences it had evolved against them. Dana Blumenthal of the U.S.D.A. marked the “very compelling examples and evidence that EICA can occur,” in meeting of Ecological Society of America (ESA, 2004). Absence of herbivores may result in selection for the loss of costly herbivore-resistance traits, which are expected to show a trade-off with vigour or competitive ability (the evolution of increased competitive ability, or EICA, hypothesis). Statstny et al. (2005) demonstrated through his garden experiment that increased competitive ability of invasive plants may be associated with changes in resistance as well as tolerance to herbivory, and both types of anti-herbivore defence may need to be examined simultaneously to advance our understanding of invasiveness.

The better performance of *Solidago gigantean* (Asteraceae), an invasive species in Europe, as compared to North American range may be the result of changed selection pressures, as implied by the EICA hypothesis (Jakobs et al., 2004).

In enemy-free space, resources previously used for herbivore defence become dispensable and can be reallocated to growth and reproduction. Such changes can result in the evolution of highly competitive, but less well defended genotypes (Blossey and Nötzold, 1995). Increased competitive ability can emerge not only from the growth and defence tradeoff, but also from weak co-adaptation between native and invasive species (Callaway, 2002). Callaway (2002) showed that allelopathic root interaction creates a competitive advantage for *Centaurea maculosa* in invaded North American communities, but not among species of its native range. In enemy-free space, resources previously used for herbivore defence become dispensable and can be reallocated to growth and reproduction. Such changes can result in the evolution of highly competitive, but less well defended genotypes.

2.8 Propagule pressure

Propagule pressure is extremely important factor, required initially for invasion success. Baker (1955, 1967, 1974) proposed that self-compatible plants, particularly those capable of autonomous self pollination, are most likely to be successful as colonists on account of their ability to establish populations from a single propagule after long-distance dispersal. This idea was termed ‘Baker’s Law’ by Stebbins (1957). Controlled pollination experiments carried out on 17 invasive alien plant species in South Africa revealed that 100% were either self-compatible or apomictic, and that 72% of these were capable of autonomous self pollination. The distribution of breeding systems among these invasive aliens is thus strongly skewed towards uniparental reproduction (Rambuda and Johnson, 2004). Thus Baker’s rule, which has generally been considered for short-lived herbaceous plants, may also apply to invasive shrubs and trees (Rambuda and Johnson, 2004). Insect pollination between colonizers could moderate bottleneck effects when colonization begins with a few or scattered individuals (Regal, 1977). Interplay of seed and pollen dispersal systems also play a pivotal role during initial establishment stage and further it is intimately linked with ecology as well as evolution of plant groups (Regal, 1977). The study of impact of soil parameters on invasion revealed that site history and propagule pressure may be more important in determining exotic species success than soil characteristics alone, in this vegetation community (Hill et al., 2005; Rai, 2013).

Pollination success in diverse habitats e.g. in the case of *Lantana camara, Ligustrum robustum, Mimosa pigra* through profuse nectar and prolonged flower production (Ghazoul, 2002) aid in their invasion success. *Solanum mauritianum* recovers rapidly after clearing, and previously heavily invaded cleared sites due to both prolific resprouting recovery from cut stumps and through seedling emergence from the dense soil seed bank in the more open post-clearing environment (Witkowski and Garner, 2008). Alien plants *Ligustrum robustum*, *Tibouchina herbacea*, *Lantana camara* and *Mimosa pigra* might gain the double advantage of appropriating pollinators at the expense of natives whilst ameliorating seed predation simply by virtue of relatively higher seed set (Ghazoul, 2002). At community level, the overwhelming effects of ecological factors spatially covarying with diversity, such as propagule supply, make the most diverse communities most likely to be invaded (Levine, 2000). In *Prosopis juliflora,* production of many, small and hard seeds capable of surviving passage through the digestive system of animals, entering into the soil to form soil seed banks and remaining viable until favourable conditions for germination and seedling establishment appear (Shiferaw et al., 2004)

In contrast with the aforesaid findings, Bellingham et al. (2004) investigated the association of plant species invasiveness with seedling relative growth rate and survival, among 33 naturalized woody plant species in four families (Fabaceae, Mimosaceae, Pinaceae, Rosaceae), however, failed to find a consistent theoretical positive relationship and hypothesized that simple life history trait such as seedling relative growth rate provides a general explanation for patterns of plant invasion success in disturbed habitats.

2.9 Competition (plant-plant interaction)

Plant-plant interaction should also be taken into account in invasion ecology particularly in the context of competition (Callaway, 1995; Brooker, 2006). Invasive species evolve in response to their interactions with natives as well as in response to the new abiotic environment and concomitantly alter the evolutionary pathway of native species by competitive exclusion, niche displacement, hybridization, introgression, predation, and ultimately extinction (Mooney and Cleland, 2001; Rai, 2013).

Competitive plant–plant interactions commonly play a central role in invasion ecology (Brooker, 2006). Obligate mutualistic relationships among species are ubiquitous and central to ecological function and the maintenance of biodiversity (Palmer et al., 2008; Zhang, 2014; Zhang et al., 2014). The extensive review of Traveset and Richardson (2006) concluded that invasive species frequently cause profound disruptions to plant reproductive mutualisms.

Generally, invasive species are not dominant competitors in their natural systems, but competitively eradicate their new neighbours as revealed in case of *Centaurea diffusa*, a noxious weed in N. America, observed to be more aggressively competing on grass species from N. America than on closely related grass species from communities to which *Centaurea* is native (Callaway and Aschehoug, 2000).

Brooker (2006) in his critical review correlated plant-plant interaction with global environmental change and emphasized that competition plays a central role in mediating the impacts of atmospheric nitrogen deposition, increased atmospheric carbon dioxide concentrations, climate change and invasive nonnative species. For example, in the native dry forest ecosystems of Hawaii, the dense roots and shoots of invading grass species negatively affect nutrient and water acquisition and germination of native woodland species (D’Antonio and Vitousek, 1992; Cabin et al., 2002; Brooker, 2006), whilst in Californian coastal chaparral communities the invasive *Carpobrotus edulis* reduces soil water availability to native shrubs, negatively affecting their growth and reproduction (D’Antonio and Mahall, 1991; Brooker 2006). In both these cases the type of interaction is one that the native species will have experienced before, i.e. diffuse competition for resources such as water or nutrients (Brooker, 2006). Positive relationship between fitness and population size (density) in small populations, i.e., Allee effect (Allee, 1931), is a mechanism by which plant– plant interactions might have a selective impact. At low densities, reduced seed set and recruitment can occur as a consequence of pollen limitation (Antonovics and Levin, 1980; Davis et al., 2004; Brooker 2006; Rai, 2013). Flexibility in behavior, and mutualistic interactions, can aid in the success of invaders in their new environment (Mooney and Cleland, 2001).

Vila and Wiener (2004) reviewed pair-wise experiments between invading and native plant species in order to test the hypothesis that invasive plants often appear to be more competitive than native species. Most importantly it has been suggested that the influence of an invading species on total plant community biomass is an important clue in understanding the role of competition in a plant invasion (Vila and Wiener, 2004).

2.10 Role of aboveground and belowground communities

In terrestrial ecosystems, soil microbes are important regulators of plant diversity as well as affecting invasion, especially in nutrient poor ecosystems where plant symbionts are responsible for the acquisition of limiting nutrients (van der Heijden et al., 2008). The 9th biennial meeting of the Soil Ecology Society held in Palm Springs, CA in May 2003, addressed the theme of ‘‘Invasive species and soil ecology’’ (Bohlen, 2006; Rai, 2013).

In invasion ecology, aboveground and belowground communities can be powerful mutual drivers, with both positive and negative feedbacks (Grime, 2001; Wardle et al., 2004). However, belowground invasions may be equally widespread. Exploring links between above and belowground communities illuminates the broader ecological implications of species invasions (Wardle, 2002).

Root-associated organisms and their consumers influence plants more directly, and they also influence the quality, direction, and flow of energy and nutrients between plants and decomposers. Exploration of the interface between population- and ecosystem-level ecology is an area attracting much attention (Wardley et al., 2004) and requires explicit consideration of the aboveground and belowground subsystems and their interactions. Invasive plants can also alter ecological interactions in the rhizosphere leading to important but poorly understood consequences for microbial dynamics, nutrient uptake and competitive interactions in the plant community (Bohlen, 2006).

Soil biota in some invaded ecosystems may promote ‘exotic’ invasion, and plant–soil feedback processes are also important (Callaway et al., 2004). Two of the most economically and ecologically damaging invasive plants on North American rangelands are diffuse knapweed (*Centaurea diffusa* Lam.) and spotted knapweed (*Centaurea maculosa* auct. Non Lam.) (Lacey et al., 1989; Roche, 1994; Sheley et al., 1998). Presently, these two Eurasian knapweeds are widely distributed across North America (Sheley et al., 1998; USDA NRCS, 2002). Relative benefit of native soil communities to two native plants and two knapweeds i.e. diffuse (*Centaurea diffusa* Lam.) and spotted knapweed (*Centaurea maculosa* auct. non Lam.) and the growth of these plants in soil from knapweed infestations and from adjacent native rangelands were investigated in North America (Meiman et al., 2006). Meiman et al., (2006) observed that native soil community appeared to be more beneficial to spotted knapweed than to the other plants studied, including diffuse knapweed. Therefore, it appears that two closely related knapweeds have very different interactions with soil biota and perhaps different strategies for invasion (Meiman et al., 2006). Callaway et al. (2004) reported that soil microbes from the home range of the invasive exotic plant *Centaurea maculosa* L. have stronger inhibitory effects on its growth than soil microbes from where the weed has invaded in North America. In invaded soils, *Centaurea* cultivates soil biota with increasingly positive effects on itself, which may contribute to the success of this exotic species in North America (Callaway et al., 2004; Rai, 2013). Kornissa and Caraco (2005) applied the physical theory for nucleation of spatial systems to a lattice-based model of competition between plant species, a resident and an invader, and the analysis reaches conclusions that differ qualitatively from the standard ecological theories.

Callaway et al. (2008) found that one of North America's most aggressive invaders of undisturbed forest understories, *Alliaria petiolata* (garlic mustard) which inhibits mycorrhizal fungal mutualists of North American native plants, has far stronger inhibitory effects on mycorrhizas in invaded North American soils (attributed to specific flavonoid fractions in *A. petiolata* extracts) than on mycorrhizas in European soils where *A. petiolata* is native.

Mangla et al. (2008) demonstrated a new pathway/mechanism on experimenting with microbial role (*Fusarium semitectum*) in rhizosphere soils of *Chromolaena odorata* and on native species which indicated that the impacts of this severe tropical weed are due to the exacerbation of biotic interactions among native plants and native soil biota rather than just enemy release or novel interaction hypothesis.

One of the most apparent and dramatic examples of belowground invaders is the invasion of northern forest by non-native earthworm species, a subject that has received much attention in recent years (Bohlen et al., 2004a, 2004b; Bohlen, 2006). In the case of earthworms, much of their effect occurs because of their role as ecosystem engineers capable of substantially changing the physical and chemical characteristics of the soil environment, with consequences for the entire soil food web, nutrient distribution, and even vertebrate and understory plant communities (Bohlen, 2006). Species-site characteristics actually determine the impact of the invasive weed plants on the soil microfauna rather than invasive/ native species in isolation (Yeates and Williams, 2001; Rai, 2013).

Microcosm investigations indicated that the composition of the arbuscular mycorrhizal fungi (AMF) community belowground can influence the structure of the plant community aboveground, and may play a role in facilitating or repelling invasion (Stampe and Daehler, 2003; Rai, 2013).

In plant invasion also study of this interrelationship (aboveground/belowground-invasion) is imperative (Wardle et al., 2004). A combined aboveground-belowground approach to community and ecosystem ecology is enhancing our understanding of the regulation and functional significance of biodiversity and of the environmental impacts of human-induced global change phenomena (Wardley et al., 2004; Rai, 2013).

Soil microbes have profound negative and beneficial effects on plants through pathogenic effects, root–fungus mutualisms and by driving the nutrient cycles on which plants depend (Callaway et al., 2004). Callaway et al., (2004) demonstrated that soil microbes from the home range of the invasive exotic plant *Centaurea maculosa* L. have stronger inhibitory effects on its growth than soil microbes from where the weed has invaded in North America. Therefore, *Centaurea* and soil microbes participate in different plant–soil feedback processes at home compared with outside *Centaurea*'s home range. In native European soils, *Centaurea* cultivates soil biota with increasingly negative effects on the weed's growth, possibly leading to its control. But in soils from North America, *Centaurea* cultivates soil biota with increasingly positive effects on itself, which may contribute to the success of this exotic species in North America (Callaway et al., 2004; Rai, 2013).

Root-derived natural products play an important role pertaining to interactions between plants and soilborne organisms, by serving as signals for initiation of symbioses with rhizobia and mycorrhizal fungi

(Field et al., 2006). They may also contribute to competitiveness of invasive plant species by inhibiting the growth of neighbouring plants through the mechanism of Allelopathy (Field et al., 2006). It has been demonstrated through various researches that the ability to produce allelopathic chemicals may contribute to success of invasive plants (Whittaker and Feeney, 1971; Rice, 1974; Williamson, 1990; Callaway and Aschehoug, 2000; Inderjit and Duke, 2003; Callaway et al., 2005; Field et al., 2006; Inderjit et al., 2006; Rai, 2013).

Root-derived natural products play an important role pertaining to interactions between plants and soilborne organisms, by serving as signals for initiation of symbioses with rhizobia and mycorrhizal fungi (Field et al., 2006). They may also contribute to competitiveness of invasive plant species by inhibiting the growth of neighbouring plants through the mechanism of Allelopathy (Field et al., 2006). It has been demonstrated through various researches that the ability to produce allelopathic chemicals may contribute to success of invasive plants (Whittaker and Feeney, 1971; Rice, 1974; Williamson, 1990; Callaway and Aschehoug, 2000; Inderjit and Duke, 2003; Callaway et al., 2005; Field et al., 2006; Inderjit et al., 2008; Rai, 2013).

2.11 Insurance Hypothesis

Increasing domination of ecosystems by humans is steadily transforming them into *depauperate systems* (Loreau et al., 2001). A major future challenge is to determine how biodiversity dynamics, ecosystem processes, and abiotic factors interact. The insurance hypothesis (Yachi and Loreau, 1999) propose that biodiversity provides an “insurance” or a buffer, against environmental fluctuations, because different species respond differently to these fluctuations, leading to more predictable aggregate community or ecosystem properties (Yachi and Loreau, 1999; Loreau et al., 2001). Microbial microcosm experiments show less variability in ecosystem processes in communities with greater species richness, perhaps because every species has a slightly different response to its physical and biotic environment (Naeem and Li, 1997; Rai, 2013).

2.12 Diversity Resistance Hypothesis

Biological invasions are a pervasive and costly environmental problem that has been the focus of intense management and research activities over the past half century (Kennedy et al., 2002). The diversity resistance hypothesis, which argues that diverse communities are highly competitive and readily resist invasion, is supported by both theory and experimental studies conducted at small spatial scales (Elton 1958; Crawley, 1987; Case, 1990; McGrady-Steed et al., 1997; Tilman, 1997, 1999; Levine and D’Antonio, 1999; Knops et al., 1999; Levine, 2000; Naeem et al., 2000; Symstad, 2000; Dukes, 2001; Kennedy et al., 2002; Rai, 2013).

2.13 Herbivore pressure

Intensive herbivory by ungulates can enhance exotic plant invasion, establishment (de Villalobos et al., 2011), and spread because: (1) many exotic plants are adapted to ground disturbances such as those caused by ungulate feeding, trampling, and movements; (2) many exotic plants are adapted for easy transport from one area to another by ungulates via endozoochory and epizoochory; (3) many exotic plants are not palatable or are of low palatability to ungulates, and consequently, their survival is favored as ungulates reduce or eliminate palatable, native plants (Hobbs, 1996; Augustine and McNaughton, 1998; Riggs et al., 2000; Kie and Lehmkuhl, 2001; Riggs et al., 2005; Vavra et al., 2007; Rai, 2013). In order to study how the predators impact the succession of vegetation, we derive invasion conditions under which a plant species can invade into an environment in which another plant species co-exists with a herbivore population with or without a predator population (Feng et al., 2011).

Herbivore-resistance traits of dominant plant species and impacts of “keystone” animal species cascade through the system to affect many organisms and ecosystem processes (Brown et al., 2001).

Herbivore pressure may be an important attribute facilitating the invasion process as demonstrated with the spatial pattern of colonization by the *prairie* lupin, *Lupinus lepidus*, which is governed by herbivore pressure. The plants are eaten by the leaf-tying larvae (caterpillars) of several lepidopteran species, and there is evidence for thresholds in the parameter ranges of plant spatial extent and timing of initial colonization that predict whether the herbivores can halt the invasion (Chin, 2005). As well as providing fresh insight into the dynamics of successional systems, these findings are relevant to the control of invasive plants because they suggest the possibility of developing protocols for the most effective timing and spatial deployment of herbivorous control agents (Chin, 2005). Results of Clay et al. (2005) have broad implications for understanding the success of invasive species. They mentioned that plants invading novel habitats may frequently suffer less damage from pests and parasites than native species. Further, in their experiment, the relative biomass of infected tall fescue was enhanced by herbivores, suggesting that this grass may be better able to invade novel habitats with high levels of herbivore pressure. Moreover, their results confirmed the important role of mammalian herbivores in shaping the composition and dynamics of plant communities (Clay et al., 2005; Rai, 2013). Parker et al., (2006) performed meta-analysis of 63 manipulative field studies including more than 100 exotic plant species which revealed that native herbivores provide biotic resistance to plant invasions, but the widespread replacement of native with exotic herbivores eliminates this ecosystem service, facilitates plant invasions, and triggers an invasional ‘‘meltdown.’’

Ecological factors like fire often increases the abundance and diversity of exotics (Hughes et al., 1991; Milberg and Lamont, 1995; D’Antonio et al., 2000), resulting in a positive feedback enhancing the dominance of the exotic grasses and more intense fires (D’Antonio and Vitousek, 1992) (Fig. 3), as demonstrated in forest of Amazon basin. Invasive African grasses in the Amazon are having highly flammable litter leading to forest fire and hence conversion of forests to grass land/savannah. Land use change leads to less carbon sequestration and hence contributing to global climate change (Fig. 3).

In addition to aforesaid ecological attributes/ hypotheses/ theories, Raffaeli (2004) mentioned certain attributes which may be equally applicable to biodiversity loss emanating from invasive species. Attributes such as body size and its related characteristics such as home range and tolerance to stress, together with differences in species richness between trophic levels, will determine the impact on ecosystems of different biodiversity loss scenarios (Raffaelli, 2004).

2.14 Evolutionary aspect

Despite the increasing biological and economic impacts of invasive species, little is known about the evolutionary mechanisms that favour geographic range expansion and evolution of invasiveness in introduced species (Sax et al., 2005; Lavergne and Molofsky, 2007; Rai, 2013). Eco-evolutionary consequences of climate change and role of the emerging synthetic discipline of evolutionary community ecology is predicted to have a profound impact on future biodiversity (Lavergne et al., 2010; Rai, 2013). Lavergne and Molofsky (2007) focused on the genetic and evolutionary aspects of invasive species through study on wetland grass *Phalaris arundinacea* L. in North America demonstrating rapid selection of genotypes with higher vegetative colonization ability and phenotypic plasticity and hence tendency to evolve in response to changing climate. Further, multiple immigration events of *Phalaris arundinacea* L., thus trigger future adaptation and geographic spread of a species population by preventing genetic bottlenecks and generating genetic novelties through recombination (Lavergne and Molofsky, 2007; Rai, 2013). Using a phylogenetic supertree of all grass species in California, Strauss et al. (2006) showed that highly invasive grass species are, on average, significantly less related to native grasses than are introduced but noninvasive grasses.

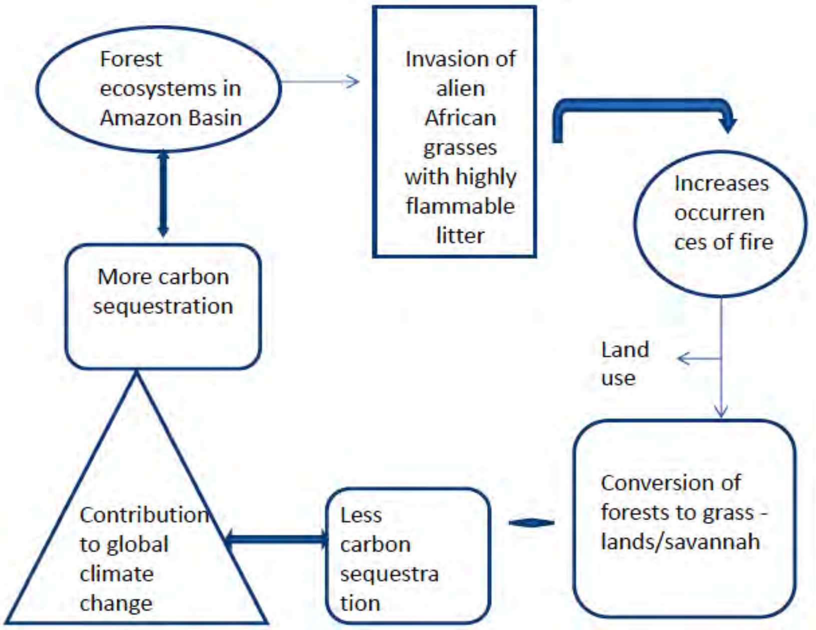

Fig. 3 Interface of invasion with land use and global climate change (Modified after D'Antonio and Vitousek, 1992; Mack et al., 2000; Rai, 2013).

Charles Elton (1958) stated that ‘‘we must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora. If newcomers arrive from far away as the result of large-scale alterations in geography or climate, the change in selective regime and the evolutionary responses to this change could be dramatic.’’ (Mooney and Cleland. 2001; Rai, 2013).

Evolutionary aspect of invasive species also drew attention of researchers (Lee, 2002; Rai, 2013). Further, workshop on the Evolutionary Perspective of Biological Invasions in Terrestrial Ecosystems was held in Halle, Germany from 30 September to 3 October 2002 which discussed evolutionary issues pertaining to invasive species at a length. To mention a few outcomes of conference, Bernd Blossey from Cornell University, Ithaca, USA demonstrated that *Lythrum salicaria*, introduced individuals exhibited greater biomass than did their ancestral genotypes and were less resistant to, or tolerant of herbivores. William Rogers (Rice University, Houston, TX, USA) demonstrated increased competitive ability of invasive populations of the tree *Sapium sebiferum* and elimination of this advantage when herbivores from the native range are abundant. Klaas Vrieling (University of Leiden, the Netherlands) presented a special twist of the EICA concept, showing that invasive populations of Asteraceae *Senecio jacobaea* had reduced adaptation to a specialist herbivore, but greater defence against generalist insect herbivores (Hänfling and Kollmann, 2002; Rai, 2013). Jes Pedersen, University of Copenhagen, Denmark demonstrated that Argentine ant *Linepithema humile*, share an extraordinary social structure called ‘unicoloniality’, where individuals from physically separated nests mix freely, and form supercolonies. Therefore, changes in life-history traits are also observed in invasive animals.

Recent studies (Tsutsui et al., 2000; Ellstrand and Schierenbeck 2000, Filchak et al., 2000; Krieger and Ross, 2002; Lee, 2002; Rai, 2013) suggested that the invasion success of many species might depend more heavily on their ability to respond to natural selection than on broad physiological tolerance or plasticity (Lee, 2002). Lee (2002) in his extensive review on evolutionary genetics of invasive species emphasized the utility of exploring genomic characteristics of invasive species, such as genes, gene complexes, and epistatic interactions that promote invasive behaviour. Such information could yield insights into the relationship between genetic architecture and rate of evolution, and evolutionary versus ecological factors which confer invasion success. Ellstrand and Schierenbeck (2000) in their concise review demonstrated that hybridization between species or between disparate source populations may serve as a stimulus for the evolution of invasiveness. Eurasian *Tamarix* plant species (potent novel hybrids) have spread rapidly to dominate over 600,000 riparian and wetland hectares in US (Gaskin and Schall 2002; Rai, 2013).

The extreme elevation gradients in the Hawaiian Islands provide specific opportunities for comparative studies on the ecology and evolution of temperate invaders while also creating a unique field environment for understanding interactions between temperate and tropical species (Daehler, 2005) and Daehler (2005) found that number of naturalized species declined exponentially with increasing altitude, however, in contrast, the proportion of species of European or Eurasian origin appeared to increase linearly with elevation, from 38% among all species occurring above 1200m to 53% above 2000m and 90% above 3000m.

2.15 Genetic diversity/hybridization

As we know that biodiversity is the sum total of all biotic variation from the level of genes to ecosystems (Purvis and Hector, 2000), genetic diversity is also an important factor particularly in relation to host-pathogen co-evolution and prospecting of disease resistant genes (Allen et al., 2004). Because elucidating how allelic diversity within plant genes that function to detect pathogens (resistance genes) counteracts changing structures of pathogen genes required for host invasion is critical to our understanding of the dynamics of natural plant populations (Allen et al., 2004; Rai, 2013). Genetic studies are decoding the language plants and microbes use to negotiate the symbioses and genes from both plants and microbes contribute to symbiosis (Marx, 2004). The two partners engage in a complex molecular conversation that allows the microbes to infect the plant cells and then entice the cells to undergo the developmental changes necessary for establishing the symbioses (Marx, 2004).

Willis et al. (2000) tried to test the hypothesis that increases size of certain invasive weeds is genetical rather than environmental and found that actually it is a plastic response to novel environment. Threats to biodiversity e.g. habitat fragmentation prevent sufficient dispersal of natives whereas long term dispersal in case of exotics tend to maintain their genetic connectivity and hence invasion success (Trakhtenbrot et al., 2005; Rai, 2013). Moreover, gene manipulation in different disciplines require utmost precaution as it has generated concern over the risk of producing new invasive species or exacerbating current weed problems (Parker and Kareiva, 1996).

Genetic modifications, through traditional breeding or genetic engineering, of crop or other species can potentially create changes that enhance an organism’s ability to become an invasive species (Wolfenbarger and Phifer, 2000). Although genetic engineering transfers only short sequences of DNA relative to a plant’s entire genome, the resulting phenotype, which includes the transgenic trait and possibly accompanying changes in traits, can produce an organism novel to the existing network of ecological relationships. Potential ecological impacts through invasiveness depend on existing opportunities for unintended establishment, persistence, and gene flow of an introduced organism; each of these, in turn, depends on various components of survival and reproduction of an organism or its hybrids. Few introduced organisms become invasive, yet an issue for the management of all introduced organisms, including GEOs, is how to identify those modifications that may lead to or augment invasive characteristics (Wolfenbarger and Phifer, 2000; Rai, 2013).

The transition from colonist to invader is especially enigmatic for self-incompatible species, which must find a mate to reproduce (Elam et al., 2007). Elam et al., (2007) conducted a field experiment to test whether the Allee effect affects the maternal fitness of a self-incompatible invasive species, wild radish (*Raphanus sativus*) and observed that both population size and the level of genetic relatedness among individuals influence maternal reproductive success. Even polyploids eg. hexaploids *Carthamus creticus* and *C. turkestanicus* are noxious weeds with wide but non-overlapping Mediterranean distributions (Vilatersana et al., 2007).

Demographic studies i.e. germination and seedling survivorship characteristics of hybrids between native and alien species of dandelion (*Taraxacum*) were studied and observed that *T. platycarpum* (4X) have the advantage over *T. officinale*, whose seedlings could not survive under high temperatures (Hoya et al., 2004; Rai, 2013).

2.16 Sustainable green management approach

Many invasive aquatic plants like *Eichhornia crassipes* and also terrestrial shrub *Lantana Camara* reported to be very good in heavy metal as well as particulate pollution phytoremediation (Rai, 2008, 2009, 2012; Rai and Panda, 2014). Thus, the utilization of invasive plants in pollution abatement phytotechnologies may assist in their sustainable management.

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