Plant invasions: Emerging trends and future implications

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Invasive species are a growing problem for the world, both ecologically and economically. The impact of invasive species on native species and ecosystems has been immense. Invasion is considered to be an important driver of global change. The impact on economy by these species is evident. The cost of impact which invasive species cause is now estimated to range from millions to billions of dollars and eventually it would be severe for all ecosystems. The various aspects of invasion related to ecology and economy have been summarized to give an insight into the problem and presumed solutions to invasion. Prediction of invasiveness is intricate, but economic and ecological outcome, either good or bad of species invasion, will soon pervade all countries and societies.

ORGANISMS immigrating to new localities and their descendants have been referred to as alien, adventive, exotic, introduced and non-indigenous[1]. Species whose native status and origin are not clear are called cryptogenic species[2]. A taxon can be considered successfully naturalized after overcoming geographical, environmental and reproduction barriers, while an invasive species requires, in addition, to overcome dispersal barrier within the new region[3]. According to Rejmanek[4], invasive taxa represent a subset of naturalized taxa. Invasion is usually discovered once the plant has already naturalized. The biotic invaders tend to establish a new range in which they proliferate, spread and persist to the detriment of the environment[1]. Although defined variously by different authors, we consider the definition of alien invasive species given by GISP[5] as most pertinent to the present discussion: 'Invasive alien species are non-native organisms that cause, or have the potential to cause, harm to the environment, economies, or human health'. Thus establishment and spread of these species threatens ecosystems, habitats, or species with economic/environmental harm[6].

Invasion of exotic species is among the most important global scale problems experienced by natural ecosystems. The growing human population and improved transcontinental transport have increased the scales of movement of non-indigenous organisms, and the current enhanced rate of invasion constitutes one of the most important effects that humans have had on the earth ecosystem. In the past, many of the irretrievable losses of native biodiversity have gone unrecorded, but today there is an increasing realization of the ecological costs of biological invasion. Over 40% of the species on the list of threatened and endangered species is due to invasive species[7]. Rejmanek and Randall[8] estimated that 20% or more of the plant species is non-indigenous in many continental areas and 50% or more on many islands. As many as 10% of the 260,000 vascular plant species is estimated to be potential invaders[9].

About 18% of the Indian flora constitutes adventive aliens, of which 55% is American, 10% Asian, 20% Asian and Malaysian, and 15% European and Central Asian species[10]. Although large number of exotics have become naturalized in India and have affected the distribution of native flora to some extent, only a few have conspicuously altered the vegetation patterns of the country. *Cytisus scoparius*, *Chromolaena odorata*, *Eupatorium adenophorum*, *Lantana camara*, *Mikania micrantha*, *Mimosa invisa*, *Parthenium hysterophorus* and *Prosopis juliflora* among terrestrial exotics, and *Eichhornia crassipes* and *Pistia stratiotes* among aquatics, have posed serious threat to the native flora.

All non-native species are, however, not harmful. For example, over 70% of world's food comes from just nine crops (wheat, maize, rice, potato, barley, cassava, soyabean, sugarcane and oats), each of which is cultivated far beyond its place of origin[11]. In New Zealand, 95% of export earning derives from alien species[12]. Despite all the benefits provided by non-native organisms, the invasive species are the second largest threat to biodiversity globally after habitat destruction and constitute the number one cause of species extinctions in most island states[13] (but see also refs 14, 15). The problem seems to be alarming because many of the biological invasions are effectively irreversible.

The main objective of this article is to focus on how the invasive plant species spreads, its biological characteristics and deleterious effects on ecosystem attributes, how it affects the economy of a region, and what screening systems and management options are available to deal with the problems of plant invasion.

Invasion process

The essential first step in invasion by an alien plant is its introduction to an area beyond its previous geographical range. Introduction of non-native species may occur through

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(i) accidental introduction, (ii) import for a limited purpose and subsequent escape, or deliberate introduction on a large scale[16].

Once introduced, the invader colonizes the new habitat, produces new self-perpetuating populations and is naturalized by getting incorporated into the resident flora. This is followed by spread to new locations (Figure 1). The invader is likely to exist for some time as a single or small-localized population. The concept of dormant invader has been applied to species that are present in an area for an extended period of time before becoming a significant invader. At some point of time, however, the invader will enter a period of rapid expansion both in terms of total population size, and the number and size of individual infestations. Finally, an invader will reach a stage at which it will be a major problem (Figure 2). The invasion is not necessarily a smooth process; major episodes of population expansion may be punctuated by uneventful periods. The statistical rule, known as the 10th rule, holds that 1 in 10 of imported species become introduced, 1 in 10 of those introduced become established, and 1 in 10 of those established become pests[17]. Table 1 includes examples of rapid spread of invasive species and their impact on native flora.

Biological attributes conferring invasiveness

The success of invasion is affected by various biological attributes of the species and the characteristics of the habitat that is being invaded[18]. The attributes that make some species invasive or those that make some ecosystems vulnerable to invasion and the mechanisms that underlie these processes are poorly understood.

Some of the biological attributes associated with invasive plants are summarized below.

Fitness homeostasis

The ability of an individual or population to maintain relatively constant fitness over a range of environment is fitness homeostasis. For example, *L. camara* covers an altitudinal

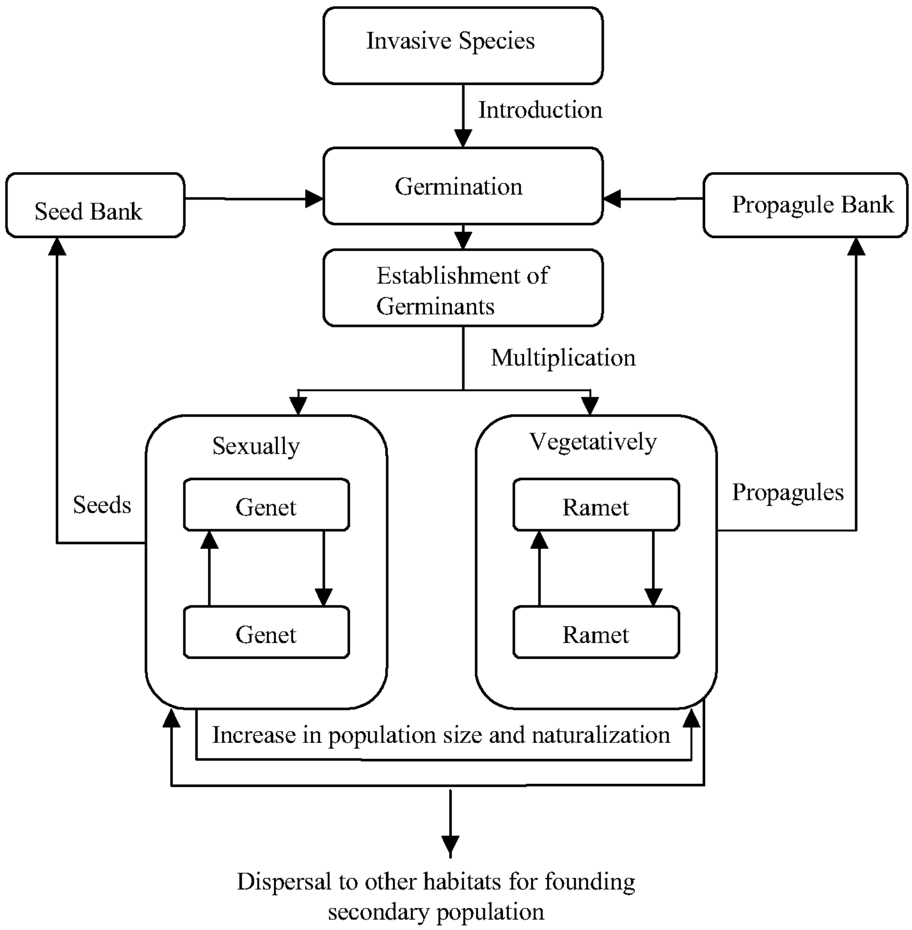

Figure 1. Recruitment model for invasive plant species. The invasive species has to overcome geographical, environmental, and reproductive barriers, face competition from indigenous species and then proceed to colonize new locations.

Table 1. Examples of spread of invasive species displacing the native flora

As much as 4×10^6 km^2 of the multilayered forest in the Amazon basin in Brazil is at risk by African grasses (*Melinis minutiflora*, *Hyparrhenia rufa*, *Panicum* sp., and *Rhynchelytrum repens*)[71].
Mimosa pigra has transformed 80 000 ha of tropical wetlands in North Australia into monotonous tall shrubland[72].
Myrica faya is native to Azores and Canary islands; it was originally brought to Hawaii by immigrants from Portugal late in the 19th century. It was first observed in Hawaii Volcanoes National Park in 1961. By 1977, it covered 600 ha of the park despite intensive control efforts and by 1985 it covered 12,200 ha of the park and 34,365 ha in the Hawaii islands[73].
Lantana infests 4 m ha in Australia and it has also infested millions of hectares of natural grazing lands in 47 countries[74].
Of the 463 grasses introduced to improve pasture in North Australia, only 5% increased pasture productivity, over 60% of the remaining species naturalized and about 13% of the introduced species survived in wild to become weed[75].
Australian paperbark tree (*Melaleuca quinquenervia*), which increased its range in south Florida by >20 ha per day and replaced other native species, now covers about 160 000 ha[76]
Miconia calvescens covers 75% of Tahiti, where it has the nickname 'the green cancer'[77].
Schinus terebinthifolius is displacing native vegetation of both uplands and wet lands in South Florida[78] and now covers 243810 ha[79].
Casuarina equisetifolia interferes with the nesting activities of turtles and American crocodiles in coastal communities of southern Florida and now infests nearly 151,065 ha[78].
Imperata cylindrica was imported into Florida in the 1940s for erosion control and as a source of forage. It failed to be useful for either purpose and now displaces native plants[80].
An important invader in the Indian subcontinent, *Parthenium hysterophorus*, has spread to virtually every state in India, and the currently infested area is estimated at 2,025,000 ha. It not only replaces native plant species, but is also a health hazard[81].

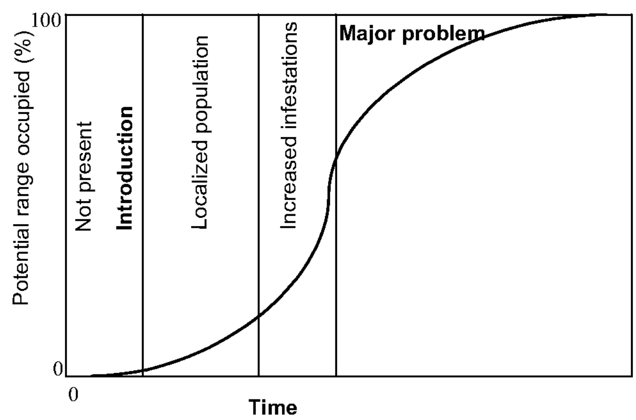

Figure 2. Diagrammatic representation of generalized phases of invasion[70].

range of up to 2000 m in the Pulnis hills, southern India[19], showing fitness homeostasis.

Seed number, size and weight

According to Rejmánek and Richardson[20], small seed weight (<50 mg), short juvenile period (<10 yrs) and short interval between large seed crops (1–4 yrs) are associated with invasiveness of woody species in disturbed landscapes. Small seed is also associated with large seed production[21], as in *P. hysterophorus*[22]. Efficient long distance (>1 km) dispersal ability also contributes to invasiveness.

Animal dispersal

Vertebrate dispersal is responsible for the success of many woody invaders in disturbed as well as undisturbed habitats[20,23]. For example, seeds of *L. camara* are widely dispersed, predominantly by fruit-eating birds, sheep, goats, cattle, foxes, jackals and monkeys, leading to its spread[24].

Geographical range

One of the likely predictors of species invasiveness is the size of the native geographical range[25–27]. This leads to potentially broad distribution over a range of distinct climate types. Forcella and Wood[25] argued that there was a positive relation between area of native distribution and invasive capacity. The propagules of the species, having widespread distribution have a high probability of transport to other countries or continents.

Alternative mode of reproduction

Vegetative reproduction is responsible for increased habitat compatibility and therefore, for successful invasion. Vegetative reproduction is particularly important for dispersal in aquatic habitats[28]. The invasiveness of *E. crassipes* is mainly attributed to its free-floating life form and asexual reproduction by stolons[29]. Similarly, the native latitudinal range of aquatic fern, *Salvinia molesta*, a species which is completely dependent on vegetative reproduction, is just 8° (24°S to 32°S; southeastern Brazil)[30], but its secondary distribution ranges from 35°S to 30°N of the equator and occupies greater diversity of the region than its native range[31]. *L. camara*, a terrestrial invader, also has enormous capability for vegetative spread and spreads through layering[24].

Competitive ability

Alien species belonging to exotic genera (and therefore possessing traits different from those of resident species) are more likely to be invasive than the alien species with native congeners[32]. Many abiotic and biotic barriers in the new environment may be overcome by plant species through non-specific mutualism (root symbionts, pollinators and seed dispersers)[33], and also with competitive superiority because of tolerance to lower resource level[34].

Allelopathy

Allelopathy is one of the several attributes of a plant permitting it to invade and establish in a new ecosystem. *L. camara* is capable of interrupting the regeneration process of native species by decreasing germination, reducing early growth rates and survival by allelopathy[35]. *P. hysterophorus* inhibits the germination and growth of other plant species due to allelopathic interactions[36]. The potentiality of *Eupatorium riparium* and *E. adenophorum* to dominate other plant species in Meghalaya has been attributed to their allelopathic properties[37,38].

Phenotypic plasticity

It is the ability of a genotype to modify its growth and development in response to changes in environment[39]. *P. hysterophorus* shows plastic response to soil quality leading to two different contrasting strategies which contribute to its success as an invader. The first strategy results in tall, fast-growing competitors with small seed mass, appropriate for rapid population expansion. The second results in short plants with high seed mass for persistence in less favourable habitat leading to slow build-up of population, with a gradual increase in size of the seed bank[40].

Habitat attributes conferring invasiveness

Habitats differ in susceptibility to invasion. However, the vulnerability of a particular habitat to invasion does not imply that any invasive plant reaching that habitat will succeed. A habitat susceptible to invasion may possess the following attributes[18]: (i) species poverty, (ii) poorly adapted native species, (iii) absence of predators, (iv) gaps generated by disturbance, and (v) presence of empty niches. Undisturbed (natural and semi natural) plant communities in mesic environments are more likely to be invaded by tall plant species[41,42]. Forest and shrub land are often invaded by short species, e.g. *Hieracium lepidulum*[43]. According to Johnstone[44], a plant can invade a site only in the absence of environmental resistance. However, a habitat characterized by disturbance is more prone to invasion than an undisturbed habitat. It is argued that the pace of invasion has accelerated during the 20th century because of rapid modification of natural habitat[13].

Hypotheses for invasion success

Based on the analysis of traits of invasive species, a number of hypotheses are proposed as a mechanism conferring invasiveness to the plants[1]. Enemy release hypothesis suggests that invaders perform better in their introduced range than their native range because they lose their enemies (often but not always parasites) during the colonization process. The evolution of increased competitive ability (EICA) hypothesis is based on the fact that exotics when liberated from their native specialist enemies, can allocate resources, otherwise used for costly traits that helped them resist those enemies, in the development of traits that provide greater competitive advantage. Whereas novel weapon hypothesis suggests that invasive plants possess novel biochemical weapons that function as unusually powerful allelopathic agents, or as mediators of new plant–soil microbial interactions[45].

Diversity–invasion dilemma

The relationship between native diversity and presence of invader in a particular ecosystem is still debatable[46]. Ecologists have long assumed that diverse landscapes are more resistant to exotic plant invaders, as their constituent species are more efficient in using up all the available resources like nitrogen and sunlight. But new studies suggest that diversity is not always a shield against invasion[46]. Different hypotheses on the relationship between native diversity and invasion are[18]:

(i) Species-poor habitats should be more susceptible to invasion than species-rich ones, an hypothesis supported on the basis of food-web theory, and the coevolution theory and empty niches. In general, small-scale studies and most of the mathematical models show a negative exponential relationship between diversity and invasion, while a few studies showed an opposite relationship.

(ii) Species-rich regions facilitate the process of invasion because of high resource availability and good growing condition at species-rich sites or interaction among native species. Analysis of worldwide data from many biomes indicated that species-rich biomes tend to have more exotic species[46]. Large-scale field studies have shown greater invasion of species-rich habitats, while a few have shown the opposite[47].

Table 2. Impact of invasion on community structure and ecosystem processes[82–87]

Plant community structure	
	Reduced species diversity in area invaded by *Heracleum mantegazzianum* compared with un-invaded region in Czech Republic.
	Lower richness of seedling and sapling in area invaded by Norway maples.
	Orbea variegata reduced diversity of annual plants and performance of chenopods in Australian shrubland. (*Orbea* impact was mediated via reduced water availability.)
	Impact of Tatarian honeysuckle on diversity and cover of native understory in New England forest due to light competition.
	A succulent perennial *Carpobrotus edulis* reduces soil-water availability to native shrub which reduces the growth and reproduction in coastal chaparral.
	Bromus tectorum invasion reduces the amount of soil-water available for other plants in Nevada grasslands.
	Reduction in competitive performance of *Fynbos* shrub due to increased nitrogen availability caused by *Acacia* invasion.
Higher trophic level	
	Increased nest predation of *Turdus migratorius* in dry deciduous forest of Illionios by introduction of *Rhamnus cathartica* and *Lonicera maakii* due to low nest height and absence of sharp thorn on exotic species.
	Himalayan *Impatiens glandulifera* produces more nectar than native *Stachys palustris* and receives more visitations by bumble-bee in Europe.
	Increase in earthworm densities under the introduced *Berberis thunbergii* and *Microstegium vimineum* than native *Vaccinium* species in New Jersey.
	Increase in earthworm densities under *Myrica faya* in Hawaii.
	Enhanced activity of feral pigs and high rate of nitrogen mineralization under *Myrica faya* in Hawaii.
	Lower richness, fewer fungi and invertebrates and higher abundance of active bacteria in site invaded by *Bromus tectorum* in Utah.
Nutrient cycling	
	Myrica and *Acacia* tend to increase available nitrogen in the system they invade in Hawaii.
	Bromus tectorum reduces nitrogen mineralization rates by having greater carbon–nitrogen and lignin–nitrogen ratios than native species, while similar litter quality effects did not explain nitrogen mineralization under invasive Hieracum in New Zealand grassland.
	Hyparrhenia rufa lowers rate of nitrogen cycling in Costa Rica.
Hydrology	
	Tamarix in southwestern North America increases evapotranspiration by 300–450 mm/yr due to high leaf area.
	Increase in water use up to 105–120 mm/yr by *Centaurea solstitialis* in annual grasslands of western North America due to its active growth period in summer.
	Decrease in community water use due to water loss by invasion of *Bromus tectorum* in New Zealand.
	Exotic annual grasses in California displace competitively deep-rooting native perennials.
	Excessive water use by *Acacia* and *Hakea* sp. in South Africa has lead to major water loss (estimated at 3×10^9 m^3/yr) and hence many rivers do not flow at all or flow only infrequently.
Fire regimes	
	Introduced grasses have increased fire frequency more than threefold in seasonally dry shrubland and woodland, effecting biodiversity in Hawaii.
	Invasion of annual grasses from the Mediterranean grasslands in desert shrubland, converting shrubland to grasslands, thereby effecting biodiversity.

(iii) There is no relationship between number of native flora and exotic species, particularly when resources are partitioned between native species and exotic species, permitting each of them to grow without hindering or promoting the other.

Ecological impact of invasive plant species

The potential for non-native species to alter ecosystem structure and function has been broadly recognized[48]. Fire regime, hydrobiological patterns, ecosystem nutrients and energy budgets can be modified, and the abundance or survival of native species can be adversely affected[1]. The pathways or mechanisms that underlie the impact of exotic plant invasion on community structure and ecosystem processes are, however, poorly understood.

Examples of the impact of invasion on ecosystem structure and processes are summarized in Table 2. To understand the impact of species invasion, it is important to understand consequences of species addition in an ecosystem. There are three possible outcomes of addition: increase, decrease or no change in ecosystem processes[49]. Increase in ecosystem processes could occur particularly in systems that have previously lost some species. Introduction of new species can also decrease the ecosystem processes[49] and can lead to deleterious effects.

Economic impact of invasive plant species

The economic impact of invasive species are both direct and indirect[50]. Direct impact reflects the effect of the invader and indirect impact implies general effects that are caused

Table 3. Economic impact due to invasion of species[52]

Species	Economic variable	Economic impact
Salt cedar (*Tamarix*)	Value of ecosystem services lost in western USA	$ 7–16 billion over 55 years
Knapweed (*Centaurea* sp.)	Impact on economy in three US states	$ 40.5 million per year direct cost
Leaf spurge (*Euphorbia escula*)	Impact on economy in three US states	$ 89 million indirect cost
Six weed species	Cost of control in Australian agroecosystems	$ 105 million per year
Pinus, *Hakea* and *Acacia*	Cost for restoring South African fynbos to pristine conditions	$ 2 billion
Eichhornia crassipes	Cost of clearing in seven African countries	$ 20–50 million per year
Varroa mite	Economic cost to bee-keeping in New Zealand	$ 267–602 million

by the presence of the invader, which could affect public health. In 2001, FAO identified six types of economic impacts of invasion: (i) on production, (ii) on price and market effects, (iii) on trade, (iv) on food security and nutrition, (v) on human health and environment, and (vi) financial cost impacts. The cost of invasive species is estimated to range from millions to billions of dollars annually[51]. Some examples[52] are illustrated in Table 3.

Heavy impacts of invaders can be exemplified by the fact that the eastern North American deciduous forests have suffered more due to invading pests and pathogens than from pollution and acid rain[53]. Invasive species bring about large-scale transformation at landscape level and cause management problems for reserve managers, either because the defined management goal cannot be achieved or because financial and manpower resources are limited[54]. Ramakrishnan[55] has discussed ecological, socio-economic and cultural aspects of the problem of biological invasion in the tropics.

Many people who seek to introduce a non-native species into a new habitat do so for an economic reason[52], and most cases of invasiveness can thus be linked to the intended or unintended consequences of economic activities[56]. This has often resulted in significant environmental, economic, health and social problems, imposing costs in billions of dollars and seriously affecting a large number of people[13]. Although it is agreed that invasive alien species have many negative impacts in human economic interests, considerable uncertainty exists about the total economic costs of invasion.

Methodologies have been developed to assess the value of non-marketed environmental and health effects[57]. The most appropriate methods for valuation of non-marketed biological resources focus on their local opportunity cost and their impact on the range of services provided by the affected ecosystem[58]. For example, according to Perrings *et al.*[59], the total economic value (TEV) of biodiversity can be evaluated using the following expression:

$$\mathrm{TEV} = f(\mathrm{DUV}, \mathrm{IUV}, \mathrm{OV}, \mathrm{QOV}, \mathrm{BV}, \mathrm{EV}),$$

where DUV is direct use value (comprising consumptive and productive use values) , IUV is indirect use value, OV is optional value, QOV is quasi optional value, BV is bequest value, and EV is existence value. It may be argued that if the process of invasion continues with the current pace, there would be overall reshuffling in the values of DUV, IUV, OV, QOV, BV, EV. Therefore, TEV of biodiversity will also change in the future. According to Levine and Antonio[60], ecological and economic cost associated with human-caused biological invasion may continue to rise substantially over the coming years and decades. This calls for proper management strategies that could lead to reduction of economic cost associated with biological invasion.

Management strategies

Screening system

For the development of management strategies, it is essential to examine the introduced species in order to predict their potential for invasion through a reliable screening system. During the past decade, several screening systems were independently developed for predicting invasive plants in specific regions of the world. For example, Reichard and Hamilton[61] developed a screening system for woody plant invasion in North America, Tucker and Richardson[62] did so for woody plant invasion in South Africa, and Pheloung[63] for woody and herbaceous plant invasion in Australia. All screening systems require answering a series of questions on attributes such as life-history, biogeography, habitat and weed history[64]. The answers permit a species to be classified as likely to be invasive or unlikely to be invasive. These screening systems correctly identified 79–98% of the known invasive plants within the region for which they were designed[65], and 60–93% for the Hawaiian islands[64] (Table 4). Developing screening systems that could be applied with minor modifications, to different regions may be a more efficient approach[65].

Management tools

Management strategies employed against invasive plants can be divided into two basic groups, viz. protectionist and interventionist. Protectionist strategies attempt to retain particular ecosystem in a hypothetical 'natural' or pristine state by preventing invasions which usually contain a strong legislative element. However, the interventionist strategy is an attempt to suppress or remove existing invaders

Table 4. Predictivity of region-specific screening tools for invaders

Screening system	Predicted invasiveness within region[65] (%)	Comparison of correct predictions for known invasive species of Hawaiian islands[64] (%)
North American system for woody invaders[61]	85	82
South African system for woody invaders[62]	79	60
Australian system for woody and herbaceous invaders[63]	98	93

from a particular habitat, thereby reducing their population size to a more acceptable level and minimizing their impact on ecosystem functioning. For control of the invasive plant species, manual, mechanical, chemical and biological control methods may be applied. However, all the control strategies have drawbacks associated with them. Manual removal is a labour-intensive and low-efficiency technique. Mechanical control involves usually mechanized or power-driven equipments, but the process is inefficient in dealing with extensive invasion and in undulating terrain. Chemical control involves the use of inorganic/organic herbicides. A serious disadvantage is the prohibitively high cost of most of the chemical control programmes. Safety to other plant species is, in addition, of paramount importance when using herbicides to control invasive species. Often the success of biological control programme is not clear-cut, because complete control is only achieved in some years and/or at some locations[66]. In India, the biocontrol agent (*Teleonemia scrupulosa*) released for *Lantana* control failed since the control agent could not cope with the vigorous regrowth of *Lantana* at the onset of monsoon rains, or the control agent itself suffered heavy mortality during winter months[67].

Scaled-up, spatially explicit individual-based model studies indicate that the most rapid and cost-effective management strategy for the control of invasive plants would be to first clear low-density stands of juvenile plants followed by higher density stands of juvenile plants and then high density stands of adult plants[68]. Country-specific development of such models is desirable.

Future perspectives

Substantial progress has been made in past 15 years in generating information on risks of invasive species. For example, an international effort conducted under Scientific Committee on Problems of Environment (SCOPE) gave a great international visibility, and induced local initiatives to cope with the problem of invasion. Interest in biological invasion has been driven both by practical problems and by intrinsic lessons to be learned from organisms migrating and succeeding in new environment[55,69]. The Convention on Biological Diversity in the 8th Article calls on governments 'to prevent the introduction of, control or eradicate, those alien species which threaten ecosystem, habitat or species'. Co-operation among the countries in data acquisition and sharing will be necessary. Prediction of invasiveness is complicated, but attempts to forecast the possibility of an introduced organism becoming invasive need to be pursued. The economic and ecological consequences, both good and bad, of species invasion everywhere should become an important concern to all members of the society. The ecosystem level consequences of invasion are, however, still little understood and there is an urgent need of studies on biological invasions in India. Public awareness of environmental change and degradation, and widespread concerns for the development of sustainable system of land use have to be combined with the awareness of the effects of invasive species on the system to create a promising environment in which researches on species invasion can be promoted and funded.

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