

Plant Invasion - A Contemporary Ecological Concern

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ABSTRACT

Man's propensity for modifying his environment and introducing alien species has largely overcome the barriers to invasion that were previously imposed by geographical isolation. The dramatic increase in both the numbers and extent of plant invasions in the recent past are a direct consequence of man's activities, because of which biological invasion of alien plants is one of the contemporary concerns of ecology as it degrades resources, alters ecosystem processes, affects trophic levels and leads to endangerment and extinction of native species. Thus, invasion of habitats by non-native species has serious consequences for ecological, economic, and social systems.

In Kashmir Himalayas also, a number of non-native plant species are fast spreading and there is an urgent need to identify such invasive species and the habitats they are likely to encroach upon. Although there is no single trait which can be used to predict the invasive potential of either native or exotic plant species, success during the reproductive stage may be necessary for successful colonization followed by expansion into natural communities which depends on diaspore production, dispersal and establishment. A systematic study of such invasive species is of particular interest as it will throw light on their demographic characteristics, allelopathic potential, growth characteristics, resource allocation pattern, reproductive capacity and other attributes which make them invasive and obnoxious. The information generated would be useful for planning and formulating effective strategies for their control.

Keywords: Plant invasion, ecological basis, economic impact, *Anthemis cotula*, Invasiveness, Invasibility.

INTRODUCTION

Biological invasions have been common in natural ecosystems over evolutionary time and have had significant effects on the composition of and interactions within the resulting communities (Mooney and Drake, 1989). However, the advent of human populations and associated development of mechanized transport between population centres has provided an unparalleled opportunity for organisms to cross physical barriers that would have been impossible to traverse naturally. Humans, therefore, are not only altering the mechanism for biological invasions but through land use

and habitat disturbance are also transforming the physical environment within which invaders act and potentially succeed. This is providing new ecological landscapes for invasions that favour organisms with the attributes that make them successful in disturbed and/or variable systems. The net result, according to Mooney and Drake (1989), is the creation of a "new biological order" with favoured organisms being found in increasing abundances all around the globe which is evident by the escalating number of naturalised non-indigenous plant species in most regions of the world (Sykora, 1990; Rejmanek and Randall, 1994; Mack and Lonsdale, 2001; Pimental *et al.*, 2001). A number of biotic, abiotic and anthropogenic factors affect the process of invasion (Burke and Grime, 1996; Mack, 2000). The factors that promote plant invasions include natural and human-mediated disturbances (Fox and Fox, 1986; Crawley, 1987; Hobbs, 1989), release of immigrant species from the constraints imposed by their native co-evolved natural enemies upon introduction to a new area (Maron and Vila, 2001), enhanced competitive advantage in the new environment (Vitousek and Walker, 1989), and synergistic interactions among invaders (Simberloff and Von Holle, 1999).

This global phenomenon of invasion of habitats by non-native species has serious ecological and economic costs (Dukes and Mooney, 1999; Pimental *et al.*, 2000) and invasive species are now viewed as a significant component of global change (Vitousek *et al.*, 1996). The impact of invasive species on native species, communities, and ecosystems has been widely recognized (Wilcove *et al.*, 1998; Parker *et al.*, 1999; Stein *et al.*, 2000; Sakai *et al.*, 2001) and ecosystem-level effects of invasive species are being actively pursued (Vitousek and Walker, 1989; Mooney and Hobbs, 2000). Documented ecological effects of invasive plants include competitive suppression of native species (Busch and Smith, 1995; Huenneke and Thomson, 1995; D'Antonio and Mahall, 1991; Melgoza *et al.*, 1990), altered fire or water regimes (Cronk and Fuller, 1995; Hobbs and Huenneke, 1992), and changed nutrient status of soils (Mooney and Drake, 1989). Economic losses due to alien species have been widely reported and according to one estimate the annual economic impact of invasive species in the United States, United Kingdom, Australia, South Africa, India and Brazil is more than 314 billion US dollars (Pimental *et al.*, 2001).

In view of the above mentioned ecological and economics costs, a new sub-discipline of invasion ecology has emerged (Alpert *et al.*, 2000) that has organised itself around three main topics: invasiveness, invasibility and impacts which are briefly reviewed below.

THE INVASION PROCESS OF PLANTS

The process of invasion by plants has been intensively described and discussed

among researchers, and various sub-divisions of the process have been proposed (di Castri, 1989; Williamson, 1989; Williamson and Fitter, 1996). A recently developed model of the idealized plant invasion (Heger, 2001) is appealing in its approach because of its logical sub-division of the process and because it distinguishes between the stages in the plant invasion and the steps (processes) leading to each stage. The first step is immigration, in which propagules of the species are deliberately or accidentally introduced to a new area (stage 1). If at least one propagule is able to grow and reproduce unaided by humans, the species is defined as being spontaneously established (stage 2). Some species are able to form a population and if the population reaches a minimum viable population size (MVP), it is more resistant to environmental, demographic and genetic stochastic forces, and is described as being permanently established (stage 3). Some of the permanently established plant species are able to spread into new localities of the new range (stage 4). There is not yet agreement among researchers on the terminology for describing the status of non-indigenous plants and the steps in the invasion process (Richardson *et al.*, 2000). In the present context the terms introduction, establishment, naturalization and outbreak/invasion for the steps in invasion (step 1-4 *sensu* Heger) and the terms introduced, established, naturalized and invasive for describing the status of the plant species (stage 1-4 *sensu* Heger) have been used. These terms closely correspond to those used by most plant invasion biologists (Richardson *et al.*, 2000). The terms *non-indigenous* and *alien* are used interchangeably to describe plants that occur in areas outside of their place of origin. The number of plant species in the different stages of the invasion process is progressively reduced. Based on empirical studies of British plants, Williamson and Fitter (1996) proposed the "tens rule" stating that approximately ten percent of the species proceed from one stage in the invasion process to the next. Other researchers have suggested percentages of varying magnitudes (Crawley, 1987; di Castri, 1989). However, since one will never know the exact number of species that has arrived to a new area and failed, and since some plant species may establish and perish without being noticed, such estimates must be considered with caution.

ECOLOGICAL BASIS OF INVASIVENESS

Life history traits that make a species invasive have been of continuing interest because of their potential predictive power. Some studies have focussed on life history traits that may predispose species to rapid population expansion whereas others have investigated how genetic structure of life history traits may provide species with either greater phenotypic plasticity or potential for rapid evolutionary change (Sakai *et al.*, 2001).

Baker (1974) discussed several traits associated with invasive species and proposed that species with many of these characteristics were more likely to be highly invasive than species with only a few of these traits. Traits promoting weediness and invasiveness included the ability to reproduce sexually and asexually, rapid growth from seeding to sexual maturity and particularly wide ecological amplitude and adaptability. Although the concept of ideal weed is cited throughout the weed literature but few empirical data exist to support or refute Baker's list of characters (Kolar and Lodge, 2001). Thebaud *et al.*, (1996) reported that species with traits of "Baker's Ideal Weed" differ in their invasiveness and according to Williamson and Brown (1986) and Roy (1990) many invasive species have only a subset of traits described by Baker and others. Noble (1989) pointed out that Baker's list is over 20 years old and needs to be revised to include eco-physiological characteristics such as photosynthetic pathways. Evidence for the importance of such traits comes from the list of The World's Worst Weeds (Holm *et al.*, 1977) where out of first 18 species, 14 species have C_4 pathway of carbon dioxide fixation. Elmore and Paul (1983) also pointed out that C_4 species appear 17 times more frequently than expected in some lists of weeds.

Analysis of exotic species introduced into Czech Republic since 1492 (Pysek *et al.*, 1995) showed that species invasion success was related to plant height, life-form competitiveness and that the sunflower family (Asteraceae) was over-represented in the exotic flora compared with native flora.

Rejmanek (1995) pointed out that invasiveness of herbaceous species was best predicted by primary native latitudinal range. Reichard and Hamilton (1997) conducted a retrospective analysis of traits of introduced woody plants to distinguish invaders and non-invaders. Daehler (1998) using discriminant analysis model, correctly classified 86% of invaders with high risk of invasiveness. These species exhibited traits like vegetative reproduction, perfect hermaphrodite flowers, lack of pre-germination seed treatment requirements, and a long period of time during which fruit was on the plant. In an analysis of global data sets, agricultural weeds tended to be herbaceous, rapidly reproducing, and abiotically dispersed species (Sakai *et al.*, 2001).

Bazzaz (1986) related traits of invasive species with the level of disturbance which he argued have strong influence over those which can otherwise also successfully invade. Consequently, regions of low disturbance will likely be more susceptible to invasion from organisms with one set of traits while regions of higher disturbance may be invaded by organisms with a distinctly different suite of characteristics. The traits of invading taxa that tend to make them successful in more disturbed habitats include: a) high population growth rate, b) relatively short life cycle, c) early

reproductive maturity, d) high reproductive allocation e) generalists (broad-niche), f) high acclimation capabilities, and g) rapid response to resource availability.

Roy (1990) proposed that the best approach for investigating traits of invaders would be one in which species are classified into functional groups with anticipated similar traits and where the focus is narrowed to particular habitat types while Crawley (1986) argued that studies on the population biology of invasive species may allow a more precise focus on specific characteristics involved in invasiveness.

Kolar and Lodge (2001) pointed out that characteristics common to successful colonists across taxa include *r*-selected life histories with attributes such as use of pioneer habitat, short generation time, high fecundity and high growth rates and ability to shift between *r* and *k* selected strategies but like Baker's characteristics of an ideal weed, many of these ideas have not been tested quantitatively.

EVOLUTIONARY GENETICS OF INVASIVE SPECIES

The evolutionary genetics of invasive species has been relatively unexplored, but could offer insights into mechanisms of invasions (Lee, 2002). Invasions frequently constitute rapid evolutionary events (Reznick and Ghalambor, 2001), resulting in populations that are genetically dynamic over both space and time. Genetic characteristics of populations have profound impacts on their capacity for range expansion (Ellstrand and Schierenbeck, 2000 and Krieger and Ross, 2002). Both natural selection and genetic drift alter genetic structures of invading populations in ways that modify their tolerance or behaviour (Lee, 2002). Mounting evidence supports the importance of genetic attributes for invasion success, such as additive genetic variance (Pappert *et al.*, 2000), epistasis (Bradshaw and Holzapfel, 2000; Wolf *et al.*, 2000), hybridisation (Ellstrand and Schierenbeck, 2000; Soltis and Soltis, 2000), genetic tradeoffs (Weinig, 2000), action of small number of genes (Paterson *et al.*, 1995; Linde *et al.*, 2001; Krieger and Ross, 2002) and possibly, genomic rearrangements (Soltis and Soltis, 2000). Thus, invasion success could be facilitated by the presence of genetic substrate in source populations upon which natural selection could act. In some cases, genetic drift alone has promoted successful invasion (Tsutsui *et al.*, 2000), but such cases represent exceptions rather than the rule. The studies briefly reviewed above emphasize the utility of genomic approaches for determining invasion mechanisms through analysis of gene expression, gene interactions and genomic rearrangements that are associated with invasion events.

COMMUNITY INVASIBILITY

Communities differ in their susceptibility to invasion as well as in their ecological

and evolutionary response to it but few communities are impenetrable to invasion by exotic species (Usher, 1988; Lodge, 1993 and Gordon, 1998). Studies carried out by Tilman (1997), Burke and Grime (1996), Alpert *et al.*, (2000) Mack *et al.* (2000) and Dukes (2001) to address the question of differential community invasibility reveal that at least five interacting factors viz., evolutionary history, community structure, propagule pressure, disturbance and stress account for these differences.

Two aspects of evolutionary history believed to affect the invasibility are past intensities of competition and human disturbance. Habitats in which competition has been intense over evolutionary time may have low invasibility because of high competitive ability of the natives which could outcompete potential invasives. Conversely, relaxed selection for competitive ability in isolated habitats could help explain the relatively high invasibility of islands (Loope and Mueller-Dombois, 1989). As the intensity of the anthropogenic disturbance of habitats increases world-wide, the habitats with a longer history of human disturbance may show lower invasibility because of the evolution of the natives vis-à-vis disturbance (Shmida, 1985) and it may explain as to why the Old World is less susceptible to invasion than the New World (Crosby, 1986; di Castri, 1989 and Lonsdale, 1999). In fact, di Castri (1989) proposed that Old World species have greater invasion potential than New World species.

The aspects of community structure stated to influence community invasibility include: species richness, strength of interactions between species, and assemblages of predators or pathogens (Elton, 1958; Shigesada and Kawasaki, 1997). The species richness of natives seems to be positively (Bridgewater and Backshall, 1981; Robinson *et al.*, 1995; Planty-Tabacchi *et al.*, 1996; Palmer and Maurer, 1997; Wiser *et al.*, 1998; Lonsdale, 1999; Stohlgren *et al.*, 1999) than negatively (Fox and Fox, 1986; Tilman, 1997) or not (Higgins *et al.*, 1999) correlated with the degree of invasion because species richness is promoted by factors that also promote invasion (Levine and D'Antonio, 1999) or because species identity is more important than species richness (Crawley *et al.*, 1999). In fact, Levine and D'Antonio (1999) concluded that there exists a weak empirical and theoretical support for a direct negative relationship between species richness and community invasibility. Negative interactions between native and non-native species such as competition and herbivory probably limit invasions (D'Antonio and Mahall, 1991; D'Antonio, 1993) but positive interactions between non-natives and mycorrhizal fungi (Marler *et al.*, 1999), nitrogen-fixing bacteria or seed dispersers (Richardson *et al.*, 2000), or pollinators may increase invasibility. It has been hypothesized that the communities with more specialized herbivores or more generalist mutualists like pollinators, mycorrhizal fungi and strains of *Rhizobium* might be more invulnerable which according to

Richardson *et al.*, (2000) could be one of the reasons for increased invasibility of many ecosystems.

Dispersal, according to D'Antonio *et al.*, (1999), is the most important process determining invasion success mainly because evidence suggests that given sufficient propagule pressure and favourable climate, any ecosystem can be invaded by alien species. Propagule pressure could, however, be influenced by habitat characteristics, degree of fragmentation and favourability for human activities (Alpert *et al.*, 2000). Furthermore, habitats in which physical conditions or predators tend to reduce seed longevity might be less invisable because dispersal is limited in time. In this context, species with persistent seed banks may be successful as invaders (Mitchell *et al.*, 1998).

Ecologists have long recognised that disturbance promotes exotic plant invasions. The role of disturbance in invasion has risen to the level of a "dogma" and it is considered as a pre-requisite for any invasion (D'Antonio *et al.*, 1999). Disturbance has several definitions but it implies the killing of individuals or removal of part of the biomass with consequent release of resources for other individuals (D'Antonio *et al.*, 1999). Notwithstanding the poor understanding of the role of disturbance in invasion, human-disturbed areas such as roads, clearcuts and agricultural crops usually contain highest levels of richness and abundance of invaders (Spellerberg, 1998; Hobbs, 2000 and Parendes and Jones, 2000). Not only anthropogenic disturbance, but also natural disturbance caused by fire, hurricanes, volcanic events and native ungulates provide a suitable environment for invasive plants (D'Antonio *et al.*, 1999). It should, however, be borne in mind that disturbance is not always a necessary condition for invasion (Specht *et al.*, 1977; Wisser *et al.*, 1998) and in some cases suppression of disturbance may also increase invasion. Besides, different types of disturbance can have different effects in the same habitat (Milchunas *et al.*, 1989; Smith and Knapp, 1999).

Environmental stresses like low resource availability, conditions that limit metabolism or acquisition of resources and presence of toxins (allelochemicals) have also been reported to aid in invasion. Most of the work, carried out to study the effect of nutrient availability on invasion (Davis *et al.*, 2000) suggests that low resource availability tends to limit invasion but Burke and Grime (1996) pointed out that resource availability may have relatively little effect in the absence of disturbance. Sher and Hyatt (1999) argued that disturbances that are associated with invasions alter historical patterns of turnover, or flux, of resources in an ecosystem and proposed what they called as 'Disturbed Resource-Flux Invasion Matrix' or DRIM.

ECOLOGICAL AND ECONOMIC IMPACT

The invasion of habitats by non-native species is a global phenomenon with serious ecological and economic costs (Simberloff, 1996; Dukes and Mooney, 1999; Pimental et al., 2000) and invasive species are now viewed as a significant component of global change (Vitousek *et al.*, 1996). Documented ecological effects of invasive plants include competitive suppression of native species (Busch and Smith, 1995; Huenneke and Thomson, 1995; D'Antonio and Mahall, 1991; Melgoza *et al.*, 1990), altered fire or water regimes (Cronk and Fuller, 1995; Hobbs and Huenneke, 1992), and changed nutrient status of soils (Mooney and Drake, 1989). Though biological invasion is a global phenomenon and no place on the planet Earth is free of invasive species, yet detailed economic impacts due to invasive species have been documented mostly in United States (Table 1). According to one estimate the annual economic impact of invasive species in the United States, United Kingdom, Australia, South Africa, India and Brazil is more than 314 billion US dollars (Pimentel *et al.*, 2001).

PLANT INVASION IN KASHMIR

The valley of Kashmir, like other parts of the world, is witnessing transport, establishment and spread of alien plant species. Notable examples include *Anthemis cotula*, *Erigeron canadensis*, *Galinsoga parviflora*, and *Xanthium spinosum*. These species are spreading fast with deleterious consequences for the native species and ecosystems. In view of the ecological and economic impact of such invasive species, a study was conducted on *Anthemis cotula* to identify the factors responsible for its spread which revealed that this species is at present confined to ruderal habitats with varying degrees of disturbance. Experimental studies pointed out that disturbance aids in the spread of this species by making nutrients available and by bringing the positively photoblastic achenes to the surface. The achenes are thus able to sense the environmental conditions and if other conditions like moisture availability and optimal temperature prevail, mass recruitment of seedlings occurs during autumn. A minor pulse of recruitment was recorded during spring also. Thus, a temporal variability in germination time and recruitment occurs which represents an ecological trade-off between survival and fecundity in relation to seedling emergence time, as striking differences in survivorship and fecundity among pre- and post-winter populations were observed. This phenotypic variation in the life history trait of emergence time, is ecologically and evolutionarily important due to its effect in determining species fitness. In *A. cotula*, environmental control of emergence seems evident but the existence of genetic variation in emergence time needs to be determined.

Table 1. Indicative costs of some alien invasive species (costs in US \$)

Species	Economic Variable	Economic Impact	Reference	
Introduced organisms	disease	Annual cost to human, plant, animal health in USA	\$41 billion per year	Daszak <i>et al.</i> , 2000
A sample of alien species of plants and animals		Economic costs of damage in USA	\$31 billion per year	Pimental <i>et al.</i> , 2000
Salt Cedar (Tamarix)		Value of ecosystem services lost in western USA	\$7-16 billion over 55 years	Zavaleta, 2000
Knapweed (<i>Centaurea</i> spp.) and leafy spurge (<i>Euphorbia esula</i>)		Impact on economy in three US states	\$40.5 million per year direct costs; \$89 million indirect costs	Bangsund <i>et al.</i> , 1999; Hirsch and Leitch, 1996
Most serious invasive alien plant species		Costs 1983-92 of herbicide control in Britain	\$344 million/year for 12 species	Williamson, 1998
Six weed species		Costs in Australian agroecosystems	\$105 million/year	CSIRO 1997 Cited in Watkinson, Freckleton and Dowling, 2000
Pinus, Hakea, Acacia, and lowland acacias		Costs on South African Fynbos to restore pristine conditions	\$2 billion	Turpie and Heydenrych, 2000
Rabbits (<i>Oryctolagus</i>)		Costs in Australia	\$373 million/year (agricultural)	Wilson, 1995 cited in White and Newton-Cross, 2000
Golden apple snail (<i>Pomacea</i>)	snail	Impact on rice in the Philippines	\$28-45 million/year	Naylor, 1996

Analysis of the growth characteristics of the species point towards a faster growth rate and higher resource allocation to aboveground parts particularly leaves and reproductive organs. Higher allocation to leaves is especially significant in view of the production of water soluble allelochemicals by the leaves which in laboratory bioassays caused inhibition of seed germination and seedling characteristics of a wide variety of species. On the contrary, the allelochemicals at low concentrations (1000 ppm) promoted achene germination of the species. The broad strategy adopted by the species in its successful invasion is diagrammatically shown in the Fig. 1.

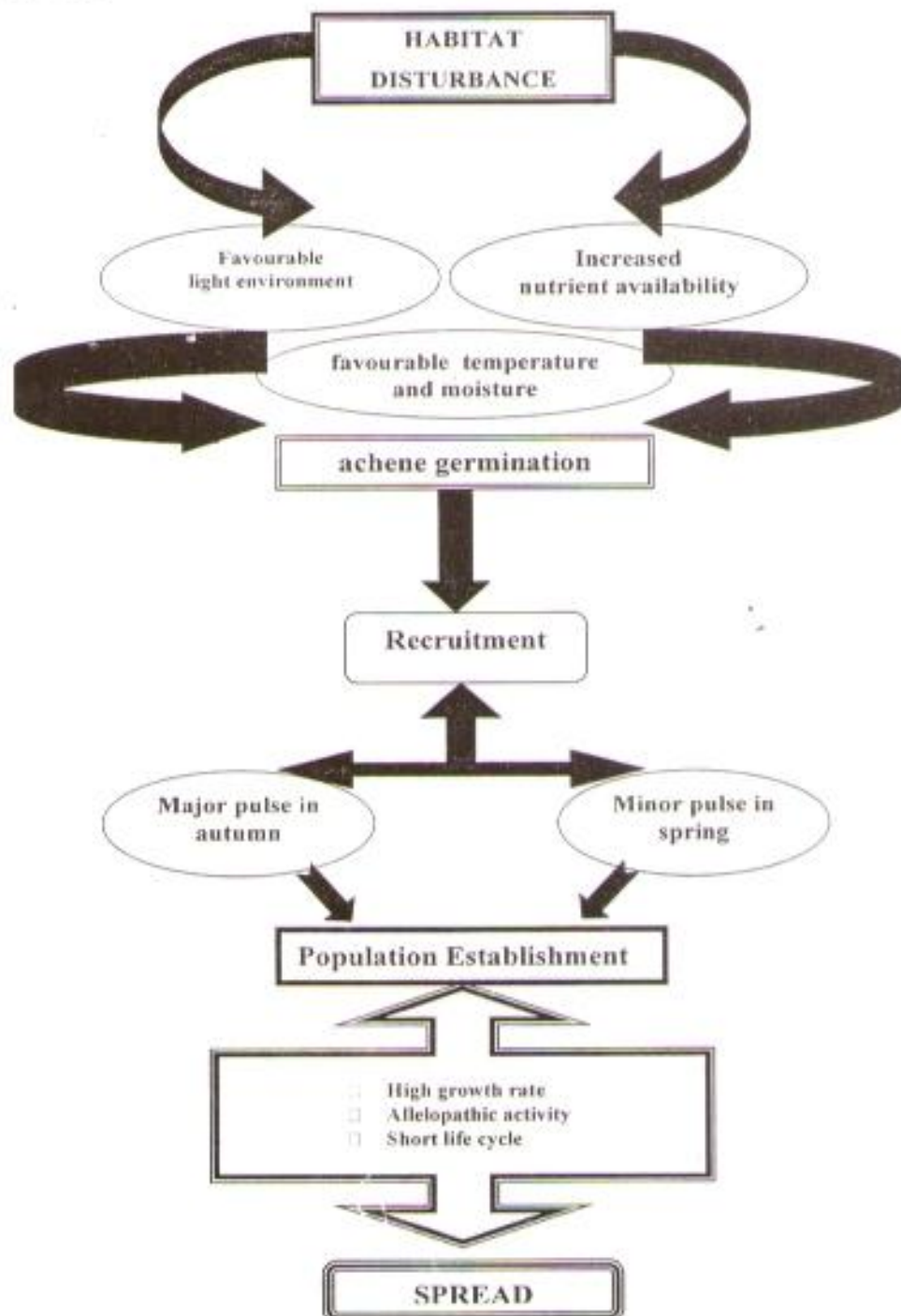


Fig. 1. Diagrammatic representation of the traits leading to the establishment and spread of *Anthemis cotula*

CONCLUSION

The continued homogenisation of the world's flora and fauna, which represents at least millions of years of separate evolutionary histories, is an ecological holocaust of major proportions. In examining the ecological interactions of invasive non-indigenous plants and animals with native biotic communities, the introductions of non-indigenous species seem tantamount to an ecological surprise attack. To meet the challenge of established non-indigenous species and future introductions of non-indigenous species requires policy development, enforcement, education, and research. The most critical need is in the area of policy development and enforcement, supported by aggressive public awareness and educational campaigns. Public awareness of the ecological, economic, and health risks from nonindigenous species is essential to successful implementation of policy and enforcement.

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