Chapter 30

A COMPENDIUM OF ESSENTIAL CONCEPTS AND TERMINOLOGY IN INVASION ECOLOGY

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30.1 INTRODUCTION

This chapter provides a list of definitions of selected concepts and terms used in invasion ecology. Many of these have been used in different ways by different authors. The uncritical use of terms and concepts is hampering conceptual advances in some parts of the field and is impeding the smooth flow of research results into management and policy arenas. There are geographical and historical differences in the usage of terminology, some of which are attributable to the origin of terms in languages other than English. Differences also exist in the use of terms for different taxonomic groups and between terrestrial, freshwater and marine systems. The schemes proposed so far are usually restricted taxonomically, or refer specifically to either terrestrial or aquatic environments. The list provided here is not exhaustive, but includes important terms and concepts used in this book and elsewhere in the current literature that may be unfamiliar to all readers and for which a clearer understanding is needed. Key references are given where appropriate. We are grateful to many colleagues for inputs and useful discussions on the evolving list, and especially to Spencer Barrett and Phil Hulme for valuable comments on a near-final version of the compendium.

30.2 THE WAY AHEAD

Quine (1936) remarked that, 'the less a science has advanced the more its terminology tends to rest upon an uncritical assumption of mutual understanding.' As much of the present volume emphasizes, invasion science is a young discipline with comparatively shallow roots, and with literally thousands of papers appearing only in the past 25 years. The result has been both a welcome cornucopia of questions, hypotheses and insights, accompanied by an often opaque panoply of definitions that focus on taxon- and habitat-specific phenomena that have not strived to seek the more fundamental ecological and evolutionary threads that bind these elements together. As such, considerable 'license and creativity' (see Carlton 2002) now accompany the terminology of the science, as reflected in the many different definitions excavated by Falk-Petersen et al. (2006) and as discussed below. It is our view that a lack of stabilization of fundamental concepts impedes both the science and management of alien species.

In 1958 a famous international symposium was held in Italy on the 'Classification of Brackish Waters'. This meeting produced one of the rare international conventions ('The Venice System for the Classification of Marine Waters') that for many decades led to an increased level of clarity and a reduced level of misunderstanding among those studying estuaries around the world. As with all such conventions, it was not without a difficult birth, and it has been continually critiqued and refined in the past 50 years. While the glossary presented in this chapter was not precipitated by such an international convention seeking consensus, we believe that we reflect here much (but certainly not all) of the general agreements and disagreements among many leading workers in the field. We propose that the definitions presented here should act as stage-setters from which we can now proceed. Generating a uniform, broadly accepted and acceptable set of terms and concepts for invasion science, which while acknowledging the debates within and conflicting perceptions (often generated by differing spatial and temporal scales) universal to all science, will, we argue, profoundly advance the discipline. Without a common language on the *science* side, translating the critical aspects of why concerns about the prevention and management of alien species are fundamental to both the environment and ecosystem services on the *policy* side will often remain confused and confusing to the public, the press and the political world.

The way ahead is to seek both consensus and concession among the broadest possible realm of invasion scientists.

30.3 OVERVIEW OF CONCEPTS

The concepts are presented in the form of a glossary. Terms in bold type indicate cross-references to other concepts in the list.

Alien species (synonyms: adventive, exotic, foreign, introduced, non-indigenous, non-native) – Those whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers (i.e. human-mediated extra-range dispersal). Some **alien species** (a small proportion) form self-replacing populations in the new region (see **tens rule**). Of these, a subset has the capacity to spread over substantial distances from **introduction** sites. Depending on their status within the **naturalization–invasion continuum**, **alien species** may be objectively classified as **casual**, **naturalized** or **invasive** (Richardson et al. 2000b; Pyšek et al. 2004). Note: designation of a species as alien should include a statement about the region under discussion; depending on the scale of observation, a species can be alien to a country but native to the continent (see discussion in Lambdon et al. 2008).

Baker's rule (also called Baker's law) – For plants and some animals, the notion that organisms capable of uniparental reproduction are more likely to establish populations after **long-distance dispersal** than are organisms that require mates because they are obligately outcrossing. This originated with the following statement by Baker (1955): '*With self-compatible individuals a single propagule is sufficient to start a sexually-reproducing colony, making its establishment much more likely than if the chance growth of two self-incompatible yet cross-compatible individuals sufficiently close together spatially and temporally is required.*' (see Barrett, this volume).

Biological invasions (synonyms: bioinvasions, biotic invasions, species invasions) – The phenomenon of, and suite of processes involved in determining, the following: (i) the transport of organisms, through human activity (intentionally or accidentally, through **introduction pathways**) to areas outside the potential range of those organisms as defined by their natural dispersal mechanisms and biogeographical barriers; and (ii) the fate of such organisms in their new ranges, including their ability to survive, establish, reproduce, disperse, spread, proliferate, interact with **resident** biota and exert influence in many ways on and in invaded ecosystems. There is a school of thought that advocates that the concept of **biological invasions** should more broadly embrace both **range expansions** (involving no obvious human mediation), because the fundamental processes (except, critically, the means of negotiating a major biogeographical barrier (Wilson et al. 2009a)) are the same (both involve the movement of individuals from a donor community into a recipient community (Sorte et al. 2010)) see discussion under **dispersal pathway**. Cf. **range expansions**.

Biosecurity – The management of risks posed by organisms to the economy, environment and human health through exclusion (the prevention of initial **introduction** of a species), mitigation, adaptation, control and **eradication** (Hulme, this volume).

Biotic acceptance (synonym: 'The rich get richer' concept) – A notion that argues that the dominant general pattern in invasion ecology at multiple spatial scales is one where natural ecosystems tend to accommodate the establishment and coexistence of **alien species** despite the presence and abundance of **native species** (i.e. the opposite of what we would expect from the **biotic resistance** hypothesis). At large spatial scales, the same abiotic conditions that promote high diversity of **native species** (energy, substrate and habitat heterogeneity, etc.) also support diverse floras of **alien species**. The patterns of **invasibility** may be more closely related to the degree of resources available in **native** plant communities, independent of species richness. (Stohlgren et al. 1999, 2006). Most treatments discuss only species richness within the same trophic level as the **alien species**. However, because cross-taxon facilitation and inhibition are crucial mediators of **invasibility**, a broader consideration of biodiversity is appropriate (Richardson et al. 2000a). Much remains to be understood about these hypotheses across habitats and taxa; for example, see Leprieur et al. (2008), who found no support for either **biotic acceptance** or **biotic resistance** among global freshwater fish invasions. Cf. **biotic resistance**.

Biotic homogenization – The addition to, and often the partial if not extensive replacement of, local biotas by **alien species** (see McKinney & Lockwood 1999), which can result in decreased compositional turnover (β-diversity) of species between distant areas, both in terms of taxonomic and phylogenetic similarity (Winter et al. 2009).

Biotic resistance – Resistance by **resident species** to the establishment (or post-establishment survival, proliferation and spread) of **alien species**. A classic hypothesis, first articulated by Charles Elton (1958) (the **diversity–invasibility hypothesis**), is that **biotic resistance** is greater in more diverse communities. Most evidence for **biotic resistance** comes from experimental work using synthetic assemblages that vary in diversity, and from modelling (Tilman 1999). Empirical tests of the effects of species richness on **invasibility** have produced unambiguous results (Levine & D'Antonio 1999). The hypothesis is usually tested by exploring the relationship between the numbers of **native** and **alien species**, which appears negative (supporting **biotic resistance**) at very small spatial scales but positive at larger scales (more **alien species** in areas with high richness of **native species**) where it led to the formulation of a '**biotic acceptance**' concept (Stohlgren et al. 2006). This discrepancy, termed the '**invasion paradox**' by Fridley et al. (2007), is largely explained by the spatial scale of observation (Fridley et al. 2004; Herben et al. 2004) and by covarying external factors (Shea & Chesson 2002).

Casual species – Those **alien species** that do not form self-replacing populations in the invaded region and whose persistence depends on repeated **introductions** of propagules (Richardson et al. 2000b; Pyšek et al. 2004). The term is generally used for plants.

Colonization pressure – A recent variant of the concept of **propagule pressure**; defined as the number of species introduced or released to a single location, some of which will go on to establish a self-sustaining population and some of which will not. Lockwood et al. (2009) argue that **colonization pressure** should serve as a null hypothesis for understanding temporal or spatial differences in **alien species** richness, as the more species are introduced, the more we should expect to establish. They show that **propagule pressure** is related to **colonization pressure**, but in a nonlinear manner (see also Blackburn et al., this volume).

Competitive release hypothesis – A hypothesis that predicts that **alien species** may be released from competition in habitats with novel competitors or no competitors (Sorte et al. 2010); part of several competition models in **invasion ecology** also related to the **evolution of increased competitive ability hypothesis** (**EICA**), which predicts increased competitive ability through the relaxation of herbivore pressure.

Corridor – As used in **invasion ecology**, a dispersal route (a physical connection of suitable habitats) linking previously unconnected regions (Hulme et al. 2008; Wilson et al. 2009b) (see **dispersal pathway**; **introduction pathway**; **vector**).

Cryptogenic species – Species of unknown biogeographical history which cannot be ascribed as being **native** or **alien** (Carlton 1996a; see also Carlton 2009 for a discussion of the misapplication of the concept). Species can be recognized as clearly alien (based upon palaeontological, archaeological, historical, biogeographic, vector, genetic and other evidence), although their geographic origin may be unknown; these are not **cryptogenic species**.

Darwin's naturalization hypothesis – The notion than **alien** species with close **native** relatives in their introduced range may have reduced chances of establishment and **invasion**; based on ideas formulated by Charles Darwin (1859) in chapter 3 of *The Origin of Species*, borrowing ideas from Alphonse de Candolle, in the context of his discussion on the 'struggle for existence' between similar organisms: '*As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera*' (Daehler 2001a; Procheş et al. 2008; Thuiller et al. 2010).

Dispersal pathway – The combination of processes and opportunities resulting in the movement of propagules from one area to another, including aspects of the **vectors** involved, features of the original and recipient environments, and the nature and timing of what exactly is moved. The definition thus combines phenomenological and mechanistic aspects. Wilson et al. (2009b) define six types of **dispersal pathway**: leading edge; corridor; jump dispersal; extreme **long-distance dispersal**; mass dispersal; and cultivation. Human mediation is only essential in the last two of these categories (which form a sub-group: **introduction pathways**). This definition emphasizes that the distinction between an **invasion** and a **range expansion** is not absolute and that dispersal events are best considered as points on a continuum. Note that Carlton and Ruiz (2005) argue that the term 'pathway', as currently used in the invasion literature, means three distinctly different things: the cause of **invasion**, the geographic route and the **vector** itself. Cf. **vectors**.

Diversity–invasibility hypothesis – The proposition that more biologically diverse communities are less susceptible to **invasion** by novel species or genotypes (related terms and concepts include: biotic-resistance hypothesis; diversity-resistance hypothesis; species-richness hypothesis) (Fridley, this volume). See also **biotic acceptance**, **biotic resistance**, **invasional meltdown**.

EICA (the **evolution of increased competitive ability hypothesis**) – Predicts that plants introduced to an environment that lacks their usual herbivores (or disease agents) will experience selection favouring individuals that allocate less energy to defence and more to growth and reproduction (Blossey & Nötzold 1995).

Enemy release hypothesis (**ERH**) – Proposes that **alien species** have a better chance of establishing and becoming dominant when released from the negative effects of natural enemies that, in their native range, lead to high mortality rates and reduced productivity (Keane & Crawley 2002). Colautti et al. (2004) argue that the **ERH** is often accepted without recognizing that all **alien species** will lose at least some natural enemies owing to bottlenecks during transport. See also Dormontt et al. (this volume).

Eradication – The extirpation of an entire population of an **alien species** within a designated management unit. When a species can be declared eradicated (that is, how long a period of time after the management intervention) depends on the species and the situation and must take into account factors such as seed-bank longevity (for plants).The probability that a species should be quantified?

Feral species – **naturalized species** that have reverted to the wild from domesticated stock, i.e. have undergone some change in phenotype, genotype and/or behaviour owing to artificial selection in captivity.

Fluctuating resources theory of invasibility – A theory, formulated for plants by Davis et al. (2000), that predicts that pronounced fluctuations in resource availability enhances community **invasibility** if coinciding with the availability of sufficient propagules to initiate an **invasion**. It is based on the assumption that an invading species must have access to available resources (e.g. light, nutrients, water for plants, food, shelter, space, mates for animals) and that a species will be more successful in invading a community if it does not encounter intense competition for these resources from **resident species**. An increase in resource availability can arise from several phenomena: the rate at which resources are supplied from external sources is faster than the rate at which the **resident biota** can use them, the **resident biota's** use of resources declines or the resources themselves become more available within the community (part of patch-dynamic theory, which includes the novel creation of often large open spaces owing to abrupt physical or biological disturbance, which may eliminate all or most of the previous biota). A short-term pulse in the availability of resources can have long-term consequences once the invading species is established in the community.

Foreign – see **alien species**.

Genetically modified organism (GMO, synonym: living modified organism) – An organism that possesses a novel combination of genetic material engineered through recombinant DNA technology, and which may have adverse effects on the conservation and sustainable use of biodiversity, owing to the risk of the organism becoming **invasive**, effects on human health and other factors (CBD 2000).

Hub-and-spoke model – The concept that **alien species** expand on a local, regional or global scale owing to the continued establishment of multiple loci, which form new population epicentres (hubs) that then interface with novel dispersal routes (spokes) (Carlton 1996b). A global example would be a species being carried from one seaport (visited by a certain set of ships and shipping routes) to another seaport on a different continent (frequented by ships on different routes).

Impact – The description or quantification of how an **alien species** affects the physical, chemical and biological environment. Parker et al. (1999) proposed that **impact** should be conceptualized as the product of the range size of the invader, its average abundance per unit area across that range and the effect per individual or per biomass unit of the invader. Lockwood et al. (2007) list the following categories of **impacts** associated with **biological invasions**: genetic, individual, population, community, ecosystem, and landscape, regional and global. Another approach, used by the Millennium Ecosystem Assessment, assesses **impacts** relative to specific types of ecosystem services: supporting, regulating, provisioning and cultural (Vilà et al. 2010). Major issues relating to **impacts** of **invasive species** include their perception and recognition with reference to human value systems (Richardson et al. 2008), and the quest for a common and objective currency, including the means for translating **impacts** into financial and other costs (Pyšek & Richardson 2010; Vilà et al. 2010). A fundamental construct of properly quantifying **impact** is experimental science, rather than deductions based on assumptions or correlations (such as a **native species** declining and an **alien species** increasing, perhaps for unrelated reasons). Equally crucial is to recognize that '**impact**' is a scaled and gradational phenomenon requiring careful, replicated quantification; and that it is not a concept that can conveniently be divided into simple dichotomous bins of '**impact**' and 'no impact'.

Introduced – see **alien species**.

Introduction – Movement of a species, intentionally or accidentally, owing to human activity, from an area where it is **native** to a region outside that range ('introduced' is synonymous with **alien**). The act of an **introduction** (inoculation of propagules) may or may not lead to **invasion**.

Introduction pathway – Describes the processes that result in the **introduction** of **alien species** from one geographical location to another. Hulme et al. (2008) suggested a universal framework applicable to a wide range of taxonomic groups in terrestrial and aquatic ecosystems. **Alien species** may arrive through three broad mechanisms: importation of a commodity; arrival of a transport vector; natural spread from a neighbouring region where the species is itself alien. These three mechanisms result in six principal pathway classes: release, escape, contaminant, stowaway, corridor and unaided. **Introduction pathways** form a subset of **dispersal pathways** – those that are mediated by human activities.

Invasion – The multi-stage process whereby an **alien** organism negotiates a series of potential barriers in the **naturalization–invasion continuum** (Richardson et al. 2000b) (cf. **range expansion**).

Invasion cliff – A construct integrating community **invasibility** and **propagule pressure**, which together constitute **invasion pressure**, defined as the probability that an environment will experience an **invasion** within a specified period. The theoretical model shows that changes in **invasion pressure** can alternatively be very sensitive or very insensitive to changes in **invasibility** and/or **propagule pressure**, depending on the magnitude of the two variables as well as on their relative values. The relationship between **invasion pressure** and its two primary components is nonlinear; in a three-dimensional graph of the three variables this sensitivity is reflected by a cliff-like feature connecting areas of unlikely **invasion** with those where invasion is almost certain. **Invasion pressure** is thus best described by two relatively stable states, separated by a tipping point (Davis 2009, and this volume). This concept is important for management, because when a system is not near the **invasion cliff**, even substantial changes in invasibility and/or **propagule pressure** due to management interventions have little potential effect on the probability of **invasion**. Alternatively, relatively minor changes could dramatically influence invasion probability if the system is positioned near the **invasion cliff** (Richardson 2009).

Invasion complex – A situation where one **invasive species** facilitates, directly or indirectly, the establishment of one or more 'secondary' **alien species**, potentially with impacts greater than the sum of the individual species. An example of *direct* facilitation is an **alien** frugivorous bird promoting the spread of an alien fruit-bearing tree, as occurred in the Hawaiian Islands when **introduced** birds promoted spread of the alien tree *Morella faya* by eating its fruits and dispersing its seeds. *Indirect* facilitation involves an **alien species** modifying environmental conditions or disturbance regimes in a manner that promotes the establishment of subsequent invaders, for example soil disturbance from rooting by **alien** wild boar promotes establishment of alien plants in several ecosystems (for examples, see Richardson et al. (2000a)) (see also **invasional meltdown**) (D'Antonio 1990).

Invasion debt – A concept that posits that even if **introductions** cease (and/or other drivers of **invasion** are relaxed, e.g. **propagule pressure** is reduced), new **invasions** will continue to emerge, **naturalized species** that are present will enter the **invasion** stage and already-**invasive species** will continue to spread and cause potentially greater **impacts**, because large numbers of **alien species** are already present, many of them in a **lag phase** (Richardson, this volume).

Invasion ecology – The study of the causes and consequences of the **introduction** of organisms to areas outside their native range as governed by their dispersal mechanisms and biogeographical barriers. The field deals with all aspects relating to the **introduction** of organisms, their ability to establish, **naturalize** and **invade** in the target region, their interactions with **resident organisms** in their new location, and the consideration of costs and benefits of their presence and abundance with reference to human value systems (Richardson & van Wilgen 2004). This term is often used interchangeably with 'invasion biology' in the literature; see also **invasion science**.

Invasion paradox – A term used in at least two broad contexts in the recent literature. The most widely used meaning relates to contrasting lines of support for both negative and positive relationships between **native** biodiversity and various measures of 'success' of **alien species** (Fridley et al. 2007; see also **biotic resistance**). Sax and Brown (2000) also used the term to describe biological invasions in general, in particular: '*why are exotic organisms, which come from distant locations and have had no opportunity to adapt to the local environment, able to become established and sometimes to displace native species, which have had a long period of history in which to adapt to local conditions?*'.

Invasion pressure – The probability that an environment will experience an **invasion** within a specified period (Davis 2009). Cf. **invasion cliff**.

Invasion science (synonym: invasion research) – A term used to describe the full spectrum of fields of enquiry that address issues pertaining to **alien species** and **biological invasions**. The field embraces **invasion ecology**, but increasingly involves non-biological lines of enquiry, including economics, ethics, sociology, and inter- and transdisciplinary studies (Richardson, this volume).

Invasibility – The properties of a community, habitat or ecosystem that determine its inherent vulnerability to **invasion** (Lonsdale 1999). Early studies tended to use the concept deterministically (particular systems were deemed either invasible or not), but **invasibility** is more appropriately considered probabilistically, and the degree of **invasibility** may change markedly over time owing to, for instance, changes in biotic or abiotic features of the ecosystem. **Invasibility** is ideally measured as the survival rate of **alien species** introduced to the system, thus accounting for losses due to competition with **resident biota**, effects of enemies, chance events and other factors (Lonsdale 1999). **Invasibility** differs from the **level of invasion**, which integrates the effects of invasibility, **propagule pressure** and climate (Chytrý et al. 2008). (see also **biotic acceptance**, **biotic resistance**, **colonization pressure**, **fluctuating resources theory of Invasibility**, **invasion cliff**, **invasion complex**, **invasion pressure**, **invasiveness**, **lag phase**, **level of invasion**).

Invasional meltdown – A phenomenon whereby **alien species** facilitate one another's establishment, spread and **impacts** (Simberloff & Von Holle 1999; see Simberloff (2006) for examples and conceptual discussion).

Invasive species – **Alien** species that sustain self-replacing populations over several life cycles, produce reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of **introduction**, and have the potential to spread over long distances (Richardson et al. 2000b; Occhipinti-Ambrogi & Galil 2004; Pyšek et al. 2004). **Invasive species** are a subset of **naturalized species**; not all **naturalized species** become invasive. This definition explicitly excludes any connotation of **impact**, and is based exclusively on ecological and biogeographical criteria (for discussion, see Daehler 2001b; Rejmánek et al. 2002; Ricciardi & Cohen 2007). It should be noted that the definition supported by the World Conservation Union (IUCN), the Convention on Biological Diversity and the World Trade Organization explicitly assumes that **invasive species** cause **impacts** to the economy, environment or health (see IUCN 2000). This important difference has implications for **risk analyses** of **invasive species** (Hulme, this volume). Consequently, it is crucial for **risk assessment** protocols to assign dimensions of risk separately for elements of **invasion** and **impact**. Note: designation of a species as **invasive** should include a statement about the region under discussion; for example a species **alien** to a state can be **native** to a continent (see discussion in Lambdon et al. (2008)).

Invasiveness – The features of an **alien** organism, such as their life-history traits and modes of reproduction that define their capacity to invade, i.e. to overcome various barriers to **invasion**. The level of **invasiveness** of a species can change over time owing to, for example, changes in genetic diversity through hybridization, introgression or the continued arrival of new propagules of the same species that is already established in a region, but from new and different (meta)populations, such that genetic diversity may increase. This last concept is important in management strategies, which sometimes assume that less concern needs to be paid to the continued **introduction** of species (the continued arrival of propagules, whether accidental or intentional) that are *already* well-established in a region, overlooking the critical potential for elevated **invasiveness** over time.

Jump dispersal – A category of **long-distance dispersal**, sometimes over substantial scales, whereby connection (gene flow) between the new and original ranges is maintained. Cf. **dispersal pathway**.

Lag phase (synonym: latency period) – the time between when an **alien** species arrives in a new area and the onset of the phase of exponential increase. Multiple factors are frequently implicated in the persistence or dissolution of the **lag phase** in **invasions**, including an initial shortage of **invasible** sites, the absence or shortage of essential mutualists, inadequate genetic diversity and the relaxation of competition or predation (owing to other alterations in the **resident biota**). However, Aikio et al. (2010) show that **lag phases** may equally be the result of statistical or sampling artefacts commonly found in time series of records of **alien species**.

Lag time – The broad set of lag (the period of time from one event to another) phenomena across the entire **invasion** sequence, which may include the following: (i) the apparent long-term failure of species to **invade** successfully from potential donor regions to potential recipient regions (until they do, owing to, for example, changes in the environments of donor and/or recipient regions, to changes in vectors or to changes in other phenomena); (ii) lags in population increase (see **lag phase**); and (iii) lags in geographic expansion, whereby a species may appear to remain resident in one relatively small and restricted region for a long period of time, but then begin to suddenly expand (owing, in part, to the fact that spread increases exponentially once multiple foci have had time to establish).

Level of invasion – Actual number or proportion of **alien species** in a community, habitat or region, resulting from an interplay of its **invasibility**, **propagule pressure** and climate (Hierro et al. 2005, Chytrý et al. 2008). The **level of invasion** is determined by the product of the number of **alien species introduced** to the system (**propagule pressure**) and their survival rate, which differs in individual habitats based on their **invasibility** (Lonsdale 1999). Relatively resistant communities can be invaded to a high level if exposed to high **propagule pressure**. Even relatively vulnerable communities will experience low-level invasions if **propagule pressure** is low.

Long-distance dispersal – Dispersal of propagules over a long distance, defined either by the absolute distance travelled, or by a set proportion of all propagules that disperse the farthest. **Long-distance dispersal** occurs at various scales; extremely, propagules may move beyond the dispersal range seen over ecological timescales (Wilson et al. 2009b).

Managed relocation (synonym: assisted migration, translocation, transplantation) – A form of management intervention aimed at reducing the negative effects of global change (especially rapid climate change) on defined biological units such as populations, species or ecosystems. It involves the intentional movement of biological units from their current areas of occupancy to locations where the probability of future persistence is predicted to be higher (Richardson et al. 2009). Such movements may include **introduction** of the species to areas outside their current or known historic range; as such it potentially represents an important **introduction pathway** and its potential for causing new **invasions** is an important criticism advanced by opponents of this strategy (e.g. Ricciardi & Simberloff 2009).

Native species (synonym: indigenous species) Species that have evolved in a given area or that arrived there by natural means (through **range expansion**), without the intentional or accidental intervention of humans from an area where they are native (see Pyšek et al. 2004).

Naturalized species (synonym: established species) – Those **alien species** that sustain self-replacing populations for several life cycles or a given period of time (10 years is advocated for plants) without direct intervention by people, or despite human intervention (Richardson et al. 2000b; Pyšek et al. 2004). The term is currently mainly used with reference to terrestrial plant invasions, although it was previously widely used for mammals.

Naturalization–invasion continuum – A conceptualization of the progression of stages and phases in the status of an **alien** organism in a new environment which posits that the organism must negotiate a series of barriers. The extent to which a species is able to negotiate sequential barriers (which is mediated by **propagule pressure** and **residence time**, and which frequently involves a **lag phase**) determines the organism's status as an **alien**: **casual**, **naturalized** or **invasive species** (Richardson et al. 2000b).

Non-indigenous (**nonindigenous**) and **non-native** (**nonnative**) – see **alien species** (students should note that web searches with and without the hyphen will yield different results).

Novel ecosystems – Those comprising species that occur in combinations and relative abundances that have not occurred previously at a given location or biome. Such ecosystems result from either the degradation or **invasion** of natural ecosystems (those dominated by **native species**) or the abandonment of intensively managed systems (Hobbs et al. 2006).

Pests – A cultural term often applied to animals (not necessarily alien) that live in places where they are not wanted and which have detectable economic or environmental impact or both (Pyšek et al. 2009). Cf. **weeds**.

Propagule pressure – A concept that encompasses variation in the quantity, quality, composition and rate of supply of **alien** organisms resulting from the transport conditions and pathways between source and recipient regions (see also **colonization pressure**) (Simberloff 2009). **Propagule pressure** has emerged as a fundamental determinant of the **level of invasion**; Colautti et al. (2006) suggest that it should serve as the basis of a null model for studies of **biological invasions** when inferring process from patterns of **invasion**.

Range expansion – The process whereby a species spreads into new areas (usually new regions, rather than local-scale movements) owing to natural or human-mediated dispersal; such expansion may be assisted or primarily driven by human-mediated changes to the environment. Differs from **invasion** in that human-mediated extra-range dispersal (i.e. across a biogeographical barrier) is not implicated; the concept can be applied to both **native** and **alien species**.

Residence time – The time since the **introduction** of a species to a region; because the **introduction** date is usually derived from post-hoc records and is likely inaccurate, the term *minimum residence time* has been suggested (Rejmánek 2000). The extent of invasion of **alien species** generally increases with increasing **residence time** as species have more time to fill their potential ranges (Wilson et al. 2007; Williamson et al. 2009).

Resident biota/organisms – Species that are present in a community, habitat or region at the time of **introduction** of an **alien species**. The pool of resident species includes both **native species** and **alien species** introduced previously. (See also **biotic resistance, novel ecosystems**.)

Resource-enemy release hypothesis – Fast-growing plant species adapted to high resource availability have less constitutive defences against enemies, and therefore incur relatively large costs when enemies are present. These fast-growing species benefit most from **enemy release**, and the two mechanisms can act in concert to cause **invasion**; this could explain both the strong effects of resource availability on **invasion** and the extraordinary success of some **alien species** (see Blumenthal 2006; Blumenthal et al. 2009).

Risk assessment – The estimation of the quantitative or qualitative value of risk (the likelihood of an event occurring within a specified time frame and the consequences if it occurs). In the context of **invasion science**, **risk assessment** is undertaken to evaluate the likelihood of the entry, establishment and spread of a species (intentionally or accidentally) in a given region, negotiating given barriers in the **naturalization–invasion continuum**, and the extent and severity of ecological, social and economic **impacts** (see Hulme, this volume).

Tens rule – A probabilistic assessment of the proportion of species that reach particular stages in the **naturalization–invasion continuum**. It predicts that 10% of imported species (species brought in for cultivation or held in captivity) become **casual**, 10% of casuals become **naturalized** and 10% of **naturalized species** become pests (Williamson & Brown 1986; Williamson & Fitter 1996). The rule was developed from European plant data, but the general principle that **invasions** are rare, and that achievement of this status depends on **propagule pressure**, biology and location, holds worldwide and across all taxonomic groups, although the 10% is probably an artefact of the history of biological invasions worldwide and is likely to increase with increasing **residence times** of **alien species** in floras (Richardson & Pyšek 2006). Caley et al. (2008) point out that the **tens rule** refers to the distribution for the probability of an invader reaching a stage in the **naturalization–invasion continuum**; the point estimate 0.1 is a measure of central tendency, although it is frequently misinterpreted as a rule describing point estimates for the transition probabilities for each stage. The **tens rule** is thus not meant to be interpreted as meaning or predicting that 10% is a standard or fixed outcome of invasion probabilities. Interpretation of the **tens**

rule is also dependent on the definition and perception of *pest* species: in many cases, for example, 0% of imported species may become casual and 0% of casual species may become naturalized, or, conversely, a much larger proportion than 10% of naturalized species may be considered nuisance species, depending on the value systems assigned.

Transformers – **Invasive species** that change the character, condition, form or nature of ecosystems (Richardson et al. 2000b).

Vectors – A broadly defined phenomenon involving dispersal mechanisms that can be both non-human mediated (wind, water, birds, mammals, amphibians, etc.) and human mediated. Carlton and Ruiz (2005) propose a classification framework for the human-mediated movement of organisms that includes six elements: *cause* (why a species is transported; that is, whether accidentally or deliberately); *route* (the geographic path over which a species is transported from the origin to the destination, which they synonymize with passageway, course and corridor); *vector* (how a species is transported – that is, the physical means or agent, such as ballast, clothing, commercial oyster movement, animal feeds or vehicles; **vector** is synonymized with mode, transport mechanism, carrier, and bearer); *vector tempo* (how a given **vector** operates through time, in terms of size and rate, speed and timing: size and rate are defined as the frequency with which the **vector** operates to deliver propagules to the target region, measured as the quantity of the **vector** (in units appropriate to the **vector**) expressed per unit time (for example, gallons of ballast water per day, number of container boxes per month, etc.)); *vector biota* (quantitative and/or qualitative description of the all of the living organisms being transferred by a given **vector**, in terms of diversity, density and condition; see **propagule pressure**); and *vector strength* (the relative number or rate of established invasions that result within a specific period from a given **vector** in a particular geographic region). They note that in the invasion literature the term **pathway** can thus have very different meanings, including cause, route (corridor) and the **vector** itself. Cf. discussion at **dispersal pathway**.

Weeds – A plant is a **weed** '*if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man (without, of course, being deliberately cultivated plants)*' (Baker 1965); in cultural terms, **weeds** are plants (not necessarily **alien**) that grow in sites where they are not wanted and that have detectable economic or environmental **impacts** (Pyšek et al. 2004).

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