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Edited by Herbert H. T. Prins and Iain J. Gordon
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1 Testing hypotheses about biological invasions and Charles Darwin's two-creators rumination

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Some of today's most pressing issues deal with invasions by alien species into natural or man-made ecosystems such as agricultural landscapes. Invasions are not a new phenomenon having been a part of the relationship between man and the environment ever since humans moved out into the savannas; however, they became part of the ecological agenda in the middle of the last century. The foundations of invasion ecology stem from Charles Elton, who, in his book, *The Ecology of Invasions by Animals and Plants* (published in 1958) attempted to draw together three stands of ecology – faunal history, ecology, particularly population ecology, and conservation. Elton's book had some traction at the time (e.g. Baker and Stebbins 1965), however, few ecologists paid much attention to invasions during the 1960s even though island biogeography theory (MacArthur and Wilson 1967) did provide theoretical frameworks for how new species fitted into the resident species communities on islands. It was not until the 1970s that invasion ecology began to gain traction in the literature (e.g. Baker 1974; Embree 1979) and continues to this day (Richardson 2011). There have been recent attempts to create unified theoretical frameworks for understanding the invasion process (Blackburn *et al*. 2011) and the traits that determine the degree to which a species can invade a new ecosystem or the degree to which an ecosystem can be invaded by a new species (Richardson and Pysek 2006). These developments provide a foundation upon which to assess the degree to which hypotheses concerning biological invasions relate to real-world case studies that are proliferating in the literature.

For several reasons, Australasia, including the continent of Australia, offers a great opportunity to test hypotheses that were formulated mainly in Europe and North America. First and foremost is the fact that many excellent, scientifically trained ecologists have worked in this area of the world: clearly the legacy of Herbert Andrewartha's (1907–92), but there followed (the New Zealander) Graeme Caughley (1937–94), (the American) Eric Pianka (born 1939) and (the Canadian) Charles Krebs (born 1936). Most of the chapters in this book are written by ecologists who work in Australasia where a large amount of ecological research takes place: we could have easily doubled the number of authors if we had invited more to contribute. Second, most of Australia's

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ecologists are acutely aware of the fact that the continent is being invaded by new species, although one ecologist recently pleaded for the release of African mega-herbivores to solve Australia's fire threats (Bowman 2012), as if Australia's ecological problems are not serious enough. The science of invasion ecology has a high standing in Australia, not least because CSIRO (Commonwealth Scientific and Industrial Research Organisation) has devoted a substantial amount of resources to studying and combating biological invasions. It is not only because of ecological invasions taking place in this part of the world that we focus on Australasia (a term coined already in 1756 meaning 'south of Asia') but also because the region forms a biogeographical unit; it lies to the east of the Wallace Line and is characterised by a very peculiar flora and fauna. Indeed, Wallace's Line has been attracting the attention of biogeographers and ecologists for one-and-a-half centuries; it forms the antithesis of the concept of invasions.

The third reason is that ecological theory should be generally applicable – otherwise it is not proper theory within the realm of the natural sciences. Therefore, hypotheses, largely generated through observations of species' interactions in Laurasian ecosystems (i.e. those that evolved on the former supercontinent Laurasia in the north), should be transferable to Australasian ecosystems (which derived from the supercontinent Gondwana in the south; see Chapter 11). Due to its very isolated location, Australasia has evolved a unique flora and fauna that offers a geographic context to independently test hypotheses that were formulated elsewhere. We, as authors and editors, are aware that this comes as close as possible to testing ecology's basic tenets apart from going, literally, to the depths of the oceans. The fauna and flora of Australasia does indeed appear to come from a very different world; to quote Charles Darwin (diary for 19 January 1836):

> I had been lying on a sunny bank and was reflecting on the strange character of the animals of this country compared to the rest of the World. An unbeliever in everything beyond his own reason might exclaim, 'Surely two distinct Creators must have been at work; their object is the same and certainly the end in each case is complete'. Whilst thus thinking, I observed the conical pitfall of a Lion-Ant: a fly fell in and immediately disappeared; then came a large but unwary Ant. His struggles to escape being very violent, the little jets of sand described by Kirby were promptly directed against him. His fate however, was better than that of the fly's. Without doubt the predacious Larva belongs to the same genus but to a different species from the [European] kind. Now what would the Disbeliever say to this? Would any two workmen ever hit on so beautiful, so simple, and yet so artificial a contrivance? It cannot be thought so. The one hand has surely worked throughout the universe. A Geologist perhaps would suggest that the periods of Creation have been distinct and remote the one from the other; that the Creator rested from his labour. (Darwin on-line; see the comment on this text by Armstrong 2002).

To facilitate the reader's understanding of Australasia's uniqueness and its distinct geological and climatological history, we have included two chapters in this book, by Stannard (Chapter 11) and by McLaren and her co-authors (Chapter 12), providing information on its very long isolation from other continents. Especially for those ecologists who never have had the pleasure of visiting the unique and distinct continent of Australia and the adjacent oceanic or continental islands, these chapters may be essential for appreciating Charles Darwin's 'Two-Creators Idea'. They also provide justification for our notion that we can use Australasia as an independent test arena for evaluating ecological hypotheses that were formulated elsewhere.

The foundations of ecology

The field of ecology has been fortunate to attract some of the great minds of the eighteenth to twentieth centuries, such as Alexander von Humboldt (1769–1859; the first person who understood that vegetation varies with altitude, climate or soil, and who explored what determines the species that make up a community and their relative abundance (Stokstad 2009)), Justus von Liebig (1803–73; who discovered the Law of the Minimum), Charles Darwin (1809–82; who developed important ideas about co-existence and competition), Ernst Haeckel (1834–1919; who coined the term ‘ecology’), Alfred Wallace (1823–1913) and Eugenius Warming (1841–1924) (both fathers of biogeography), Christen Raunkiaer (1860–1938; who initiated classification of plant life-forms and who was the first quantitative ecologist), Joseph Grinnell (1877–1939; who coined the term ‘niche’) and Arthur Tansley (1871–1955; who adopted the term ‘ecosystem’ and defined it as ‘the whole system . . . including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment’). In the 1930s to 1960s a transition took place when great ecologists such as Charles Elton (1900–91; who redefined the term ‘niche’), Vero Wynne-Edwards (1906–97) and Herbert Andrewartha started long-term observations and executed carefully designed experiments to test important concepts such as density dependence. They, along with Henry Allan Gleason (1882–1975), slowly moved away from thinking about the benefit for the species, incorporating neo-Darwinian theory in highlighting the consequences of behaviour for the fitness of individuals.

The great breakthrough took place through the merger of mathematics with ecology in the work of Pierre Verhulst (1804–49; who devised the formulae for carrying capacity), Karl Pearson (1857–1936; who started looking for empirical evidence of Darwinian selection), Alfred Lotka (1880–1949; famous for his book *Elements of Physical Biology* published in 1925), Vito Volterra (1860–1940; of the Lotka–Volterra equations taken further by C. S. (Buzz) Holling in 1959), Ronald Fisher (1862–1960; famous for his book *Statistical Methods for Research Workers* (1925) and many other very important publications). This led to the golden age of ecology in the 1950s to 1960s when Evelyn Hutchinson (1903–91), Robert MacArthur (1930–72) and Edward O. Wilson (1929–) published their seminal works on ecology. It was mainly MacArthur who stressed the importance of hypothesis testing and thus was a driving force for changing ecology from a descriptive domain of knowledge (i.e. natural history) to a ‘proper’ science with an important branch, namely theoretical ecology. But, if ecology is a proper natural science, then it must follow the scientific method. This method, discovered in the seventeenth century, is described as ‘a method or procedure that has characterised natural science, consisting in systematic observation, measurement, and experiment, and the formulation, testing, and modification of hypotheses’ (*Oxford English Dictionary* online, 2013). Wikipedia explains the method further by stating:

> The chief thing which separates a scientific method of inquiry from other methods of acquiring knowledge is that scientists seek to let reality speak for itself, and contradict their theories about it when those theories are incorrect. Scientific researchers propose hypotheses as explanations of phenomena, and design experimental studies to test these hypotheses via predictions which can be derived from them. These steps must be repeatable, to guard against mistake or confusion in any particular experimenter. Theories that encompass wider domains of inquiry may bind many independently derived hypotheses together in a coherent, supportive structure. Theories, in turn, may help form new hypotheses or place groups of hypotheses into context.

Whilst the scientific method is the basis upon which the edifice of science is built, much of the field of ecology appears to be based on weak inference rather than strong inference. In weak inference there are correlations between observations that describe patterns in the world rather than structured experiments that test hypotheses about how the world works (strong inference; e.g. Horn 1971). *In science* strong inference is seen to be more powerful because weak inference is more prone to error in interpretation.

Apart from investigating invasions, in this book we also explore whether the field of ecology holds to the scientific method. In 1973 the then-president of the British Ecological Society, Amyan MacFadyen, asked the same question and his verdict, although couched carefully, was not too favourable. He wrote:

> There are those who argue that ecology, like human history, is concerned with unique events and that these are not supposed to be open to the 'scientific method'. Is this true and does 'scientific method' referred to in this context differ from its meaning in other sciences? (MacFadyen 1975)

We may fear that we enter some

> sort of nihilistic postmodern view of ecology, where there is no truth, only stories, and the choice among stories is a question of individual taste (and power). To the degree that we reject the notion of falsifiability as a criterion for ecological theory, we reject the claim of ecology to be an empirical science, and consign it to the humanities. One of the essential differences between science and other forms of knowledge is that science makes claims about the world in the form of predictions that serve as testable hypotheses. (Weiner 1995)

In this book we enshrine the notion of falsifiability to the extent that we place falsifiable hypotheses central in all the biological chapters.

A key purpose of this book is thus, to test whether modern ecological theory is based on 'the scientific method', 'strong inference' and coherent theories that have been tested, or, whether ecology remains a descriptive science, based on weak inference, correlations and ad hoc hypotheses? We, the editors, can test this because we have enough test cases in this book to evaluate this question. We thus use the field of invasion ecology as our test-bed for this investigation.

Theodoropoulos (2003) claimed invasion biology to be a pseudoscience. The problem with Theodoropoulos' attack on invasion biology, though, is that he frames his analysis not in a context of examination of evidence and theory but within psychoanalysis. We quote:

> The psychologies of prejudice and xenophobia have been well studied, and [my book] illuminates the psychopathologies that are at the root of invasion biology and why it is so uncritically

> accepted . . . Invasion biology falls into a well-studied category of paranoid belief systems known as conspiracy-theory constructs . . . The conceptual structure of invasion biology is found to be identical in all key points to those of the xenophobic, nationalist, racist, authoritarian, and fascist ideologies, and is clearly a manifestation of this common delusion, not merely an analogous belief-system. (Theodoropoulos 2003, pp. 5 and 6)

We are not inspired by this approach which uses analysis of the presumed mind-set of students of biological invasion. We are motivated by enquiries into the roots of our science by eminent scientists such as Lawton (1999: 'Are there general laws in ecology?'). Indeed, Lawton's (1999) essay is sobering for anyone who is interested in ecological theory, assembly rules and, thus, by definition, in the predictability of the outcome of biological invasions. But in essence that is what Theodoropoulos (2003, p. 189) is calling for as well: 'I invite my critics to re-examine their premises, and to begin to take in earnest the principles of scientific rigour'. This is what we seek in this book.

Invasions into and out of Australasia

Why invasion ecology? The invasion by alien species is an extremely important societal issue across all ecosystems of the world (see below). The place where the crew of Captain Abel Tasman set foot in New Zealand in 1642 is now overrun by species native to the northern hemisphere (see, e.g. Clout and Russell 2006; pers. obs.). In New Zealand as a whole the proportion of alien species in the modern vascular flora is really mind-boggling: 2536 species are naturalised exotics and 2418 species are endemic (New Zealand Plant Conservation Network 2013). In Natal, South Africa, the list of alien plant species is about 6% of the indigenous flora (310 aliens out of 4818 species in total) (Macdonald and Jarman 1985); similarly in the much smaller Golden Gate Highlands National Park, South Africa, 8% of species are aliens (64 aliens out of a total of 823 species: Daemane *et al*. 2010). In the Netherlands about 15% of the plant species are alien, most of which have arrived since the beginning of the twentieth century (233 new alien plant species out of, in total, 1604 species) (Compendium voor de Leefomgeving 2013). The alien, and potentially invasive, species list of Florida is impressive: 1413 alien plant species are recorded, which is 33% of the total list of 4283 plant species list for the state (Institute for Systematic Botany 2013; see also FLEPPC 2013). Invasive aliens are presently everywhere, even the Antarctic: Usher (1988) wrote that in the Antarctic, invasive species were not a problem. Now invading species are regularly being recorded (e.g. Tavares and deMelo 2004).

Australasia has experienced wave after wave of invading organisms, for example in Queensland some 1220 plant species are alien (*The Australian*, April 14, 2004). The Australian Government (2012) states that 'Invasive species have a major impact on Australia's environment, threatening our unique biodiversity and reducing overall species abundance and diversity'. It treats invasive species as seriously as it does terrorism: 'Environmental biosecurity is the protection of the environment and social amenity from the negative effects associated with invasive species; including weeds, pests and

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diseases. It occurs across the entire biosecurity continuum: pre-border preparedness, border protection and post-border management and control'. Similarly, New Zealand has a Biosecurity Act 1993 (see Parliamentary Counsel Office 2013), which basically gives the Governor-General unlimited powers to do anything he or she deems necessary to prevent unwanted organisms entering the country.

Yet not only is Australasia 'invaded' by alien species from outside its biogeographical region, but Australasia's unique species are also taken to other continents where they can themselves be invasive (e.g. Norman and Christidis, Chapter 5; Booth, Chapter 14). Australasia thus functions as a recipient and as a source of alien species; in that sense, Australasia is not unique. Yet this continent has some claim to uniqueness with a mammal fauna that is dominated by marsupials, in contrast to the rest of the world where placental mammals prevail or are completely supreme. Since marsupials formed a large part of the fauna of other continents in the past (e.g. in Europe: Agusti and Anton 2002, pp. 24, 69, 135) the continued present-day marsupial dominance in Australasia (not only Australia: think about the tree-kangaroos, *Dendrolagus* spp., with 12 species in New Guinea; Martin 2005) gives this biogeographical area a very special status and the recent invasion by placental mammals, therefore, has an extra poignancy.

But Australasia has more claims to uniqueness than solely the continued preponderance of marsupial species since this continent was also the birthplace of the most dominant group of birds, namely, the passerines (songbirds; Roshier and Joseph, Chapter 18). Likewise, there are many other unique organisms (for instance, eucalypts and acacias; see Miller and Burd, Chapter 2, or Tomlinson, Chapter 3) that can be threatened by invasive foreign species or can be invaders themselves. It is our contention that ecological theory must be generally true if it forms a proper part of the natural sciences, and ecological hypotheses that have generally been formulated and tested in the northern hemisphere (Martin *et al*. 2012) must be thus applicable to Australasia – unique or not. The Australasian biogeographic region thus forms an excellent 'natural laboratory' to test the generality of hypotheses about invasions and invasiveness.

The International Union for Conservation of Nature (IUCN) states that 'the spread of Invasive Alien Species (IAS) is now recognised as one of the greatest threats to the ecological and economic wellbeing of the planet. These species are causing enormous damage to biodiversity' (McNeely *et al*. 2001). Likewise, Wittenberg and Cock (2001) in their introduction to a toolkit to combat invasive species highlight the importance of the issue:

> Invasive alien species are recognised as one of the leading threats to biodiversity and also impose enormous costs on agriculture, forestry, fisheries, and other human enterprises, as well as on human health. Rapidly accelerating human trade, tourism, transport, and travel over the past century have dramatically enhanced the spread of invasive species, allowing them to surmount natural geographic barriers.

In 2009, the Executive Director of UN Environment Programme (UNEP) Mr Achim Steiner stated 'that invasive alien species may be causing over US$1.4 trillion – or 5% of the global Gross Domestic Product (GDP) – worth of damage to the worldwide economy' (Steiner 2009). On the basis of these, and similar, strong statements in (non-)governmental documents, one would expect the theoretical underpinning of invasion ecology to be profound.

Hypotheses concerning invasions

Central to the thinking and reasoning in this book is the concept of the ‘niche’. Can the niche of a species be invaded by another? If two species have similar niches, can they co-exist? There are some subtle differences concerning the way one looks at the concept of the niche, depending on whether one follows John Grinnell, Charles Elton or Evelyn Hutchinson. The Grinellian view is that the niche of an organism is determined by the habitat in which it lives (and forms the basis for habitat requirement modelling exercises to determine whether a species will be invasive or not). The Eltonian view stresses the functional attributes of the species and its position in the tropic web (and forms the basis for today’s concerns about the relationship between changes in ecosystem composition and changes in ecosystem function). In the Hutchinsonian world-view, niche is defined as an n-dimensional hypervolume where the dimensions are the resources and the environmental conditions that define the requirements of an individual or a species to live and reproduce (Hutchinson 1957, 1959). It is closely related to the Grinellian niche concept, but Hutchinson differentiated between the fundamental niche (determined mainly by the requirements of a species both physiologically and by its requirements for resources such as food) and the realised niche (the niche that is observed but which is smaller than the fundamental niche because of competition with other species). As pointed out by Soberón (2007) it is important to distinguish niche as habitat from niche as function (Whittaker *et al*. 1973; Leibold 1995). A final small point to draw attention to is the idea of the so-called ‘empty niche’: in the Grinellian definition ‘empty niches’ can occur but not so in the Eltonian (or, similarly, Hutchinsonian) niche definitions. If a species goes extinct, then in the Grinellian view a niche is left vacant and so that empty niche space can then be invaded.

The discussions about ‘niche’ have led to some very important insights. The first is the idea of ‘limiting similarity’: species cannot be too similar if they are living in the same place – if so, one of the two will go extinct, or, alternatively, natural selection will force them to become different (MacArthur and Levins 1967; Abrams 1983). From this it follows that different species cannot occupy the same niche (or guild) in the same geographic area. Species can, however, have similar ‘modes of life’, ‘ecological functions’ or ‘strategies’ but live in different areas. For example, South American rainforest primate species, though different from those of the South East Asian rainforests, occupy, broadly speaking, similar modes of life.

This book thus sets out to test a series of hypotheses that generally have a long and respectable pedigree. They are mentioned in textbooks of ecology, and are presented to undergraduate students as being ‘true’. The hypotheses are the following, and ecologists will recognise them – they are part of our domain: sometimes they are Grinellian, sometimes they are Eltonian (see below), but they are always recognisable as ‘ecological’. Do they stand scrutiny in the face of the world of Darwin’s ‘other creator’, namely, Australia, or in a wider Australasia?

The hypotheses tested in this book

Hypothesis 1: A species will not be able to invade an area that has abiotic conditions that are outside its physiological tolerance levels.

This hypothesis concerns the fundamental niche of an organism. The fundamental niche is defined, in part, by the organism's physiological tolerance of the abiotic conditions such as temperature, nutrient availability or salinity (Hutchinson 1957). In its native range the organism will have adapted to these abiotic conditions. The abiotic conditions within a non-native situation must be within the tolerance range of the organism concerned if it is to successfully invade a new ecosystem. Where this is not the case then the organism would not be able to establish viable populations.

Hypothesis 2: The extent of an invasion is negatively correlated to species diversity of functional guild competitors in the invaded environment.

This hypothesis is based upon the concept of niche space and competition and follows from Elton's (1958) ecological resistance hypothesis even though it is fundamentally Grinellian. It is hypothesised that where there are many competitor species present within an ecosystem then the niche spaces are fully occupied and an invasive organism will not be able to successfully compete for niche space within the ecosystem. However, where competitor species diversity is low, empty niche space may exist that allows the invasive organism to establish and thrive. Experiments on invasion rates into plant communities of different diversity indicate that invasive species are able to invade everywhere, but that the rate of invasion decreases with increasing species diversity (Kennedy *et al*. 2002). Further, it appears that indigenous species suppress the growth of invaders belonging to their own functional guild (Fargione *et al*. 2003). Tilman (2004) proposed that the mechanism is resource suppression of invader species by extant species in the non-native environment. Anyhow, community saturation appears to be important, and areas that contain many species are thought to be less invasible than others (Hutchinson 1959; Prins and Olff 1998; Olff *et al*. 2002; Stachowicz and Tilman 2005).

Hypothesis 3: An invasive species will not be able to replace a native species if they occupy the same niche and are in all other ways equal.

This hypothesis is related to the previous one but differs because it refers to competition between species that occupy the same niche. Where this occurs then the prediction is that, where the niche is fully occupied by the native species, the invasive species is unable to establish. The hypothesis was first formulated by Charles Darwin in his *On the Origin of Species* (1859; see Chapter 22).

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Hypothesis 4: A species will not be able to invade an area that harbours pathogens (that cause disease) or predators (that prey on the invading species) that it has not encountered before.

This hypothesis relates to the pressures that limit the ability of an invasive species to establish in a new ecosystem. Pathogens may affect the health of individuals, reducing reproductive success. Likewise, predators can sustain predation rates on populations of invasive species, which are obviously rare in the early stages of invasion, and maintain them in a ‘predator pit’ (May 1977) again increasing their susceptibility to catastrophic events. The opposite of this hypothesis is stated as the Enemy Release Hypothesis (Goeden 1971; see for reviews Keane and Crawley 2002: Liu and Stiling 2006; Blossey 2011) where the invading species is able to escape pathogens or predators that limit their population size or range extent in their native environment (e.g. Daehler and Strong 1993). An addition to the latter hypothesis is the evolution of increased competitive ability which states that a species’ invasiveness is based on its evolutionary response to natural enemy release, i.e. species shift resources previously spent on defence into traits associated with increased competitive ability (see Blossey and Notzold 1995; Wilson *et al.* 2008); see Hypothesis 7.

Hypothesis 5: A species will not be able to invade an area if its co-evolutionary species (necessary for parts of the invader’s life cycle) is/are not present in the area.

This hypothesis refers to situations where symbionts are obligatory for part of the invading organism’s life history. If the symbiont is not present in the new ecosystem or is not associated with the organism that is invading then it is unlikely that the species will be able to establish (see, for instance, Parker *et al.* 2006; for reviews see Richardson *et al.* 2000; Pringle *et al.* 2009; Van der Putten *et al.* 2010). Of course, the hypothesis is formulated in such a way that assumes that the co-evolved species, or symbiont, forms a tight species pair with the species under scrutiny (as with some orchids and their co-evolved bee species, or a particular alga and a particular fungus forming a specific lichen), even though we realise that many species do not form such tight pairs or are not strict symbionts. Indeed, in a review of invasive species, Daehler (1998) found a very significant under-representation of the Orchidaceae, known for their tight dependency on pollinators, with zero serious or widespread weeds out of some 17 500 species in the family.

Hypothesis 6: Species that occur at low population densities in their native range will not be invasive.

The hypothesis is well supported by the literature on animals (Ehrlich 1986; Crawley 1987); the observation that species that are less invasive have a low density in their native range and that invasive species have a large native range too (Moulton and Pimm 1986; Williamson and Fitter 1996). There are two parts to

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Hypothesis 6. First, the density of a species in its own range might indicate some intrinsic limitations in the capacity of the species to sustain itself in its native range. However, the rarity in the native range might be related to extrinsic factors that do not hold in the ecosystems that the organism is invading. In this case the prediction is that there will be no relationship between the population density in the native range and the invaded ecosystem. Second, the density of the species in the native range may affect the propagule pressure applied to invaded range (Williamson and Fitter 1996). Therefore, chance alone would reduce the likelihood of a rare species invading a new ecosystem.

Hypothesis 7: A species will not be able to invade an area if it has a lower use efficiency of its limiting resource than a native species that occupies the same location.

Von Liebig's (1840) Law states that an organism's growth is determined by the most limiting nutrient, not the most plentiful one. Following from this, Tilman (1985) hypothesised that resource-use efficiency structures plant communities. Where there is a limiting resource, organisms which are more efficient at using the resource will be able to sustain high population sizes and will, therefore, be able to outcompete species which occupy a similar niche. Therefore, if an invading species is more efficient at utilising limiting resources in the new ecosystem than are native species occupying the same niche then the invading species is expected to outcompete the native species and dominate the new ecosystem (see, e.g. Smith and Knapp 2001; McDowell 2002; Funk and Vitousek 2007; Drenovsky and Martin 2008; McAlpine *et al*. 2008).

Hypothesis 8: Species can more easily invade highly disturbed areas; this disturbance can be man-made or natural.

The Disturbance Hypothesis states that disturbed areas are more easily colonised because of empty niche space than are areas that lack disturbance and have a full complement of species that have packed the niche space (Connell 1978; see also Hypothesis 2) and is related to the Intermediate Disturbance Hypothesis (Grime 1973; Horn 1975; see Wilkinson 1999 for a history of the idea). The origin of the Disturbance Hypothesis is most likely Hobbs and Huenneke (1992), who state clearly that disturbance can be man-made or natural. All other things being equal then we would expect an invading species to have a greater opportunity to invade disturbed habitats than undisturbed habitats. What exactly a disturbance is, is not always clear (see, e.g. Van Andel and Van den Bergh 1987). These latter authors describe fire, grazing, soil disturbance or nutrient addition as 'disturbances' and distinguish 'direct disturbances' (those affecting the survivorship of individuals directly) and 'indirect disturbances' (those affecting resource levels or other conditions that then influence individuals in the patch). Anyhow, disturbed areas seem to be more prone to invasions than non-disturbed areas (Hobbs and Huenneke 1992; Lozon and MacIsaac 1997).