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Biotechnology

What makes a species invasive?

Swiss Agency for
the Environment,
Forests and
Landscape
SAEFL

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What makes a species invasive?

Mit deutscher Zusammenfassung
Avec résumé en français
Con riassunto in italiano

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Abstracts

E

This study summarizes the information available on species and habitat characteristics that are correlated with an increased risk of biological invasions. A number of species traits have been identified to correlate with an increased risk of invasiveness in plant and animal taxa. The best indicator for increased risk of invasiveness seems to be whether or not the species has already become invasive in another region of the world. Changes in disturbance regimes and increased resource availability are key characteristics that affect habitat invasibility. Modern forecasting models predict future invasions by exotic species with relatively high accuracy rates and provide valuable indications as to which exotic or transgenic organisms exhibit an increased invasive potential and should therefore be studied more closely.

Keywords:
exotic species, genetically modified organisms, invasiveness, invasibility, predictive models,

D

Die Studie fasst die heute vorliegenden Informationen über Eigenschaften von Arten und Habitaten zusammen, die mit einem erhöhten Risiko biologischer Invasionen korrelieren. Eine Reihe von Arteigenschaften begünstigt die Etablierung und Ausbreitung exotischer Pflanzen und Tiere. Nach heutigem Wissensstand ist der beste Hinweis auf ein erhöhtes Invasionsrisiko einer Art der Umstand, dass sie sich bereits anderswo invasiv ausgebreitet hat. Die Anfälligkeit von Habitaten gegenüber biologischen Invasionen ist am grössten bei neuen Störungen des Habitats oder bei einer Erhöhung des Nährstoffgehalts im Boden. Neuere Modelle können das Risiko von Invasionen relativ präzise voraussagen und zudem wichtige Hinweise geben, welche exotischen oder gentechnisch veränderten Arten ein erhöhtes Invasivitätspotenzial aufweisen und deshalb genauer studiert oder beobachtet werden sollten.

Stichwörter:
Exotische Organismen, gentechnisch veränderte Organismen, Invasivität, Invasibilität, Voraussagemodelle

F

La présente étude résume les informations actuelles concernant les caractéristiques des espèces et des habitats qui sont liées à un risque accru d'invasion biologique. Un certain nombre de caractéristiques liées aux espèces favorisent l'établissement et la propagation de plantes et d'animaux exotiques. Actuellement, le meilleur indicateur d'un risque accru d'invasion est la présence envahissante de l'espèce dans une autre région. Par ailleurs, les meilleurs indicateurs d'une sensibilité accrue des habitats sont la modification de la dynamique des perturbations naturelles et l'augmentation de la disponibilité des ressources. Des modèles récents permettent de prévoir le risque d'invasion avec une certaine précision. Ils donnent en outre des indications importantes sur les espèces exotiques ou génétiquement modifiées qui ont un fort pouvoir envahissant et doivent donc être plus particulièrement étudiées ou observées.

Mots-clés:
Espèces exotiques organismes génétiquement modifiés, pouvoir envahissant, modèles de prévision

I

Il presente studio riassume le informazioni aggiornate disponibili concernenti le caratteristiche delle specie e degli habitat correlate all'aumento del rischio d'invasione biologica. Un certo numero di caratteristiche delle specie favorisce l'insediamento e la diffusione della flora e della fauna esotiche. Attualmente, la presenza invasiva di una specie in un'altra regione costituisce il miglior indicatore dell'aumento del rischio di un'invasione biologica. Tuttavia, gli indicatori più significativi della maggiore sensibilità degli habitat sono la modifica della dinamica delle perturbazioni e l'aumento della disponibilità delle risorse. Modelli recenti permettono di prevedere con una certa precisione il rischio di un'invasione. Inoltre, forniscono indicazioni importanti sulle specie esotiche o geneticamente modificate che, dotate di un forte potere d'invasione, devono essere studiate o osservate con particolare attenzione.

Parole chiave:
specie esotiche,
organismi
geneticamente
modificati, invasione
biologica, modelli di
prevedere

Foreword

Genetically modified organisms may not be released into the environment, if according to the current state of knowledge the dispersal of these organisms and their new traits can not be excluded. This provision of the Gene Technology Law of 21 March 2003 implies that the potential of an organism (alien or genetically modified) to establish and spread in nature - can be recognized beforehand and be quantified.

What kind of information is needed to predict and accurately assess the level of risk of a biological invasion? Which species characteristics increase the risk of establishment and spread? How important are the characteristics of the species and how important are those of the habitat?

This study tries to give a survey of the current knowledge and experience in this field. It also shows – and this is equally important - the limits of any predictive system and warns of simplifications and early conclusions. Although there are many studies available in this field and a lot of knowledge has been acquired, there still remain numerous questions and gaps.

We would like to thank the author of this study as well as all other persons who have contributed in some way to this publication. We are convinced this study will provide an excellent science-based foundation for the implementation of the new legal provisions.

Swiss Agency for the environment,
forests and landscape

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Zusammenfassung

Einleitung

Die Einschleppung von Organismen in neue Regionen als Folge menschlicher Aktivitäten hat heute ein Ausmass angenommen, das die natürlichen Ausbreitungsprozesse bei weitem übertrifft. Auch wenn nur ein kleiner Teil der eingeschleppten Arten invasiv wird, so verursachen diese doch in ihren neuen Ausbreitungsgebieten grosse ökonomische und ökologische Schäden. Rund 10 Prozent aller verschleppten Arten werden im neuen Gebiet freigesetzt, 10 Prozent dieser freigesetzten Arten können sich etablieren, und wiederum etwa 10 Prozent dieser etablierten Arten werden invasiv. Dies bedeutet, dass rund 1 von 1000 verschleppten Arten ökologische oder ökonomische Probleme verursacht. Um diese eine invasive Art frühzeitig zu erkennen und Schäden zu vermeiden, braucht es Kriterien, die eine möglichst präzise Voraussage ermöglichen.

Biologische Invasionen laufen in der Regel in vier Schritten ab, nämlich Einfuhr, Freisetzung, Etablierung und Invasion im engeren Sinne. Die vorliegende Literaturstudie fasst die heute vorliegenden Informationen zusammen, die es über die Bedeutung der Einfuhrbedingungen, der Arteigenschaften und der Standorteigenschaften gibt.

Das erste Kapitel nennt die Ziele und beschreibt die Methodik der Studie. Kapitel 2 diskutiert Standorteigenschaften, die das Risiko einer Invasion erhöhen. Die nachfolgenden Kapitel beschäftigen sich mit Arteigenschaften, die das Risiko einer Etablierung (Kapitel 3) beziehungsweise Ausbreitung (Kapitel 4) erhöhen. Kapitel 5 stellt Modelle vor, die entweder bereits erfolgte Invasionen zu erklären versuchen oder das Risiko zukünftiger Invasionen möglichst präzise voraussagen wollen. In Kapitel 6 werden schliesslich drei Fallstudien beschrieben, die wichtige Aspekte der Risikoforschung aufzeigen sollen.

Die meisten Untersuchungen über Art- und Habitateigenschaften, die mit einem erhöhten Invasionspotenzial verbunden sind, wurden ausserhalb Europas gemacht. Die vorliegende Studie versucht herauszuarbeiten, wie weit die daraus gewonnenen Schlüsse auch für Europa gültig sind. Zudem wird die Bedeutung der Erkenntnisse aus der Forschung mit exotischen Organismen für die Risikoanalyse transgener Organismen diskutiert.

Standorteigenschaften

Die meisten Studien über Faktoren, die einen Standort mehr oder weniger anfällig für Invasionen machen, sind anhand von invasiven Pflanzen gemacht worden. Dabei ist eine Reihe von Standorteigenschaften identifiziert worden, die mit einer erhöhten Anfälligkeit für biologische Invasionen korreliert. Das Muster, das aus den in Appendix 1 aufgelisteten Studien ersichtlich wird, lässt vermuten, dass eine Erhöhung der Verfügbarkeit an Ressourcen, sei dies direkt durch Zufuhr von Ressourcen oder indirekt durch eine Änderung der Habitatstörungen, die Gefahr von

Invasionen durch gebietsfremde Pflanzenarten erhöht, da deren Wachstum primär durch die verfügbaren Ressourcen begrenzt ist.

Nur wenige Studien haben nach Standortfaktoren gesucht, die das Risiko einer Invasion durch Pilze oder Tiere erhöhen. Es ist deshalb nicht möglich, diejenigen Faktoren herauszuarbeiten, die relevant sind für Invasionen durch solche Organismen. Hinweise aus Projekten zur biologischen Schädlingskontrolle zeigen, dass einheimische Prädatoren bei der Ansiedlung von exotischen Herbivoren eine wichtige Rolle spielen.

Arteigenschaften

Es gibt eine Reihe von Eigenschaften, die mit einer erfolgreichen Etablierung und nachfolgenden Ausbreitung der Art beziehungsweise ihrer Vermehrung korreliert. So wird eine Etablierung durch all jene Eigenschaften begünstigt, die es einer Population ermöglichen, so hohe Bestandsdichten zu erreichen, dass die Gefahr des Aussterbens (zum Beispiel auf Grund stochastischer Prozesse) minimiert ist. Solche Eigenschaften sind unter anderem das Fortpflanzungssystem (z.B. asexuelle Vermehrung), die Anzahl der Nachkommen oder die Dauer des Juvenilstadiums (Appendix 3). Eigenschaften, welche die effektive Populationsgrösse (d.h. die Anzahl sich fortpflanzender Individuen) reduzieren, wie zum Beispiel sexuelle Selektion bei Tieren oder komplexe Befruchtungssysteme, sind negativ korreliert mit erfolgreicher Etablierung.

Einzelne Studien lassen vermuten, dass der Verbreitungsmechanismus etablierter exotischer Arten ein Indikator für ein erhöhtes Risiko einer Ausbreitung ist. Ebenfalls mit einer erhöhten Vemehrungs- und Ausbreitungstendenz ist zu rechnen, wenn etablierte Arten die Standortbedingungen nachhaltig ändern. So sind in letzter Zeit mehrere Studien publiziert worden, die erfolgreiche Invasionen durch exotische Pflanzenarten in Nordamerika in Zusammenhang bringen mit allelopathischen Wurzelausscheidungen, mit denen die einheimische Flora keine Erfahrung hatte. Die Bedeutung der genetischen Variabilität bei der Ausbreitung und Besiedlung neuer Lebensräume durch etablierte Arten kann noch nicht abschliessend beurteilt werden. Es ist aber zu beachten, dass einige invasive Pflanzenarten aus der Hybridisierung verschiedener Arten oder verschiedener Populationen der gleichen Art entstanden sind.

Verschiedene Faktoren, die im eigentlichen Sinne keine Arteigenschaften sind, gelten als gute Indikatoren des Invasivitätspotenzials einer Art. Der wahrscheinlich beste Indikator für eine erhöhte Gefahr einer Etablierung und Massenvermehrung ist, ob die betreffende Art beziehungsweise andere Arten der gleichen Gattung bereits in einer anderen Region der Erde invasiv geworden sind. Im Weiteren werden wiederholt die Grösse und die geographische Lage des natürlichen Verbreitungsgebietes genannt (Appendix 3). Ausserdem sind für eine erfolgreiche Etablierung die Anzahl der Einfuhren sowie die Anzahl der freigesetzten Individuen von grosser Bedeutung.

Modelle zur Risikoabschätzung von Invasionen

Verschiedene Studien haben mit mehr oder weniger grossem Erfolg versucht, rückblickend mit Hilfe von Arteigenschaften zu erklären, warum bestimmte Arten sich ausserhalb des natürlichen Verbreitungsgebiets etabliert und ausgebreitet haben. Zudem sind Modelle entwickelt worden, die die Wahrscheinlichkeit künftiger Invasionen abschätzen sollen. Da es den Anschein macht, dass für verschiedene Organismengruppen auch verschiedene Faktoren für eine Invasion verantwortlich sind, werden diese Modelle in der Regel nur für taxonomisch eingegrenzte Organismengruppen, wie z.B. Pflanzen oder Vögel, erarbeitet.

Die Modelle basieren auf qualitativen oder quantitativen Angaben über die Geschichte der Ausbreitung einer Art bzw. verwandter Arten sowie auf Angaben über die Arteigenschaften, die für die zu untersuchenden Arten als relevant für ihr Invasivitätspotenzial eingeschätzt werden. Obwohl diese Modelle heute zum Teil bereits von Behörden eingesetzt werden, sind nur wenige auf ihre Aussagekraft überprüft worden. Das grundlegende Problem bei der Voraussage des Invasivitätspotenzials neuer Arten ist, dass nur sehr wenige der eingeführten Arten invasiv werden; somit werden selbst bei einer Genauigkeit von 85 Prozent eines Modells eine grosse Zahl von Arten fälschlicherweise als invasiv eingestuft. Dies kann insbesondere dann negative Folgen haben, wenn ein Verbot der Einfuhr von fälschlicherweise als invasiv eingestuften Arten mit grossen ökonomischen Verlusten verbunden ist.

Schlussfolgerungen

Präzise Voraussagen über die Wahrscheinlichkeit, dass eine Art invasiv wird, sind und bleiben eine grosse wissenschaftliche Herausforderung. Die Tatsache, dass heute viele Risikoabschätzungsmodelle für verschiedene Organismengruppen in der Praxis eingesetzt werden, zeigt den Bedarf an biologisch validierten Systemen. In den letzten Jahren wurden Fortschritte gemacht bei der Analyse von Art- und Habitateigenschaften, die das Risiko biologischer Invasionen erhöhen und die Qualität der Modelle erreicht heute eine Voraussagegenauigkeit von bis zu 85 Prozent. Da die Dynamik kleiner freigesetzter Populationen aber von den jeweiligen lokalen Umständen abhängt, vertreten viele Experten die Ansicht, dass kaum präzisere allgemeine Voraussagen über Invasionen möglich sind. Wie genau solche Modelle sein müssen, hängt zum grossen Teil davon ab, wie gross die ökonomischen Verluste sind, die durch ein Freisetzungsverbot eines fälschlicherweise als invasiv klassifizierten Organismus anfallen. Auch wenn nie präzise vorausgesagt werden kann, welche der zahlreichen gebietsfremden Arten, die vom Menschen bewusst oder unbewusst in eine neue Region eingeführt werden, invasiv werden und welche nicht, so können Voraussagemodelle doch zumindest wertvolle Hinweise liefern, welche exotischen oder transgenen Organismen ein erhöhtes Invasivitätspotenzial aufweisen und deshalb eingehender studiert (siehe Fallbeispiele in Kapitel 6) bzw. beobachtet werden sollten.

Résumé

Introduction

La propagation d'organismes non indigènes a pris depuis quelque temps, du fait de l'activité humaine, une dimension qui dépasse de loin les processus naturels. Certaines espèces se sont largement répandues dans de nouvelles régions, entraînant ainsi d'importants dommages économiques et écologiques. Il faut cependant rappeler que seule une faible proportion des espèces deviennent envahissantes après leur importation sur un nouveau territoire: en effet, environ 10% des espèces importées se disséminent dans le nouvel habitat; 10% des espèces disséminées sont ensuite à même de s'y établir durablement; enfin, 10% seulement des espèces établies deviennent envahissantes. En somme, environ une espèce importée sur mille est susceptible de causer des problèmes écologiques ou économiques. La question centrale est de savoir dans quelle mesure il est possible de prévoir quels organismes non indigènes peuvent s'établir et, par la suite, devenir envahissants. S'il était possible de faire des prévisions relativement précises dans ce domaine, de nombreux dommages écologiques et économiques pourraient être évités.

On considère généralement que les invasions biologiques comptent quatre étapes: a) importation, b) dissémination, c) établissement, et d) invasion au sens strict du terme. Une littérature abondante décrit les particularités des organismes présentant un grand pouvoir envahissant ainsi que le rôle joué par les conditions d'importation. Ces dernières années, de grands progrès ont également été réalisés dans l'identification des caractéristiques des habitats liées à un risque accru d'invasion. La présente étude propose un panorama de l'état actuel de la recherche dans ce domaine.

Le chapitre premier énumère les objectifs de l'étude et décrit les méthodes employées. Le chapitre 2 traite des caractéristiques des habitats liées à l'augmentation du risque d'invasion. Les chapitres suivants ont pour thème les particularités des espèces participant à l'accroissement du taux d'établissement (chapitre 3) et de propagation des organismes (chapitre 4). Le chapitre 5 présente les modèles utilisés pour expliquer les invasions qui se sont produites par le passé ou pour effectuer les prévisions les plus exactes possibles concernant des invasions potentielles. Enfin, le chapitre 6 est consacré à trois études de cas traitant du risque d'invasion de certains organismes. Les aspects principaux d'une évaluation adéquate des risques seront également traités dans ce chapitre.

La plupart des études concernant les caractéristiques des organismes et des habitats présentant un pouvoir envahissant élevé ont été publiées en dehors de l'Europe. La présente étude tente de déterminer dans quelle mesure les conclusions de ces travaux sont également valables pour notre continent. Elle présente en outre l'importance des résultats de la recherche sur les espèces exotiques pour l'analyse des risques liés aux OGM.

Caractéristiques des habitats

La plupart des études concernant la fragilité des habitats face aux invasions portent sur les invasions d'espèces végétales. Elles ont permis d'identifier les caractéristiques des habitats présentant une certaine prédisposition à l'égard des invasions biologiques. Les données des études énumérées à l'annexe 1 laissent supposer qu'un accroissement de la disponibilité des ressources – qu'il soit causé par une augmentation des ressources ou par une modification de la dynamique des perturbations naturelles – entraîne une élévation du risque d'invasion par des espèces végétales non indigènes. En effet, les plantes disposent à l'origine de ressources limitées.

Seules quelques études se sont penchées sur les caractéristiques des habitats ayant une influence sur les invasions de champignons ou d'espèces animales. À l'heure actuelle, il n'est donc pas possible de recenser les facteurs jouant un rôle dans ces types d'invasions. Certains indices provenant de projets de lutte biologique contre les nuisibles permettent de penser que les prédateurs indigènes ont une importance non négligeable dans la colonisation d'un habitat par des herbivores non indigènes.

Caractéristiques des espèces

Un certain nombre de caractéristiques liées aux espèces sont en relation avec l'établissement ainsi que la propagation ou la prolifération de certaines espèces. Un établissement durable est ainsi favorisé par les facteurs permettant à une population d'atteindre une dimension telle que le danger d'extinction (provoqué, par exemple, par des phénomènes stochastiques) se trouve fortement réduit. Parmi les caractéristiques de ce type, on compte entre autres le système reproducteur (p. ex. la reproduction asexuée), le taux de reproduction ou encore la durée du stade juvénile (annexe 3). Par contre, les caractéristiques participant à la réduction de la population effective (c'est-à-dire du nombre d'individus en âge de procréer) présentent une corrélation négative avec la probabilité d'établissement. Parmi celles-ci, on compte par exemple la reproduction sexuée chez les animaux ainsi que les systèmes complexes de pollinisation.

D'après certaines études isolées, le mécanisme de propagation constitue un indicateur permettant d'estimer le risque de prolifération d'organismes non indigènes déjà établis. De même, les organismes établis ont davantage tendance à se reproduire et à proliférer lorsqu'ils modifient durablement les conditions naturelles des habitats. De fait, plusieurs études récemment publiées mettent en relation des invasions de végétaux non indigènes en Amérique du Nord avec des exsudats racinaires allélopathiques, phénomène inconnu dans la flore indigène. Il n'est pas encore possible de déterminer avec certitude l'influence de la variabilité génétique sur la propagation des espèces établies et la colonisation de nouveaux habitats. Il faut toutefois souligner que certaines plantes envahissantes sont issues d'une hybridation entre différentes espèces ou entre différentes populations de la même espèce.

Par ailleurs, une série de facteurs, qui ne sont pas à proprement parler liés à l'espèce, sont de bons indicateurs pour estimer le pouvoir envahissant d'un organisme. Par exemple, on déterminera si l'espèce concernée ou d'autres espèces du même genre ont déjà été envahissantes dans d'autres régions du globe. Ce facteur représente certainement le meilleur indicateur d'un risque accru d'établissement et de prolifération. Un autre facteur souvent rencontré est la taille et la position géographique de l'aire de répartition de l'espèce envahissante (annexe 3). Enfin, d'autres indicateurs importants pour le succès de l'établissement sont la fréquence des importations ainsi que le nombre d'individus introduits.

Modèles pour l'évaluation du risque d'invasion

Diverses études ont tenté, avec plus ou moins de succès, d'utiliser les caractéristiques des espèces pour expliquer rétrospectivement pourquoi certaines espèces plutôt que d'autres se sont établies et propagées en dehors de leur habitat naturel. Parallèlement à ces études, des modèles ont été élaborés afin d'estimer la probabilité de nouvelles invasions. Puisque les facteurs de risque semblent varier d'un groupe d'organismes à l'autre, ces modèles sont en général conçus pour des groupes déterminés, p. ex. les plantes ou les oiseaux.

Ces modèles sont fondés sur des données qualitatives ou quantitatives concernant l'historique de la propagation d'une espèce ou d'espèces parentes ainsi que sur les caractéristiques des espèces considérées comme significatives pour l'estimation de leur pouvoir envahissant. Bien que ces modèles soient parfois employés par des instituts officiels, il est rare que leur validité ait été contrôlée. En effet, la prévision du pouvoir envahissant de nouvelles espèces se heurte à un problème fondamental: un très petit nombre des espèces introduites devient effectivement envahissant. Pour cette raison, même un modèle dont les prévisions seraient exactes à 85% désignerait à tort de nombreuses espèces comme envahissantes, alors qu'elles sont en réalité inoffensives. Cet état de fait peut avoir des conséquences indésirables, en particulier si l'interdiction de l'importation d'espèces faussement désignées comme envahissantes entraîne d'importantes pertes au niveau économique.

Conclusions

À l'heure actuelle, l'établissement de prévisions exactes concernant le pouvoir envahissant d'un organisme représente toujours un défi de taille pour la communauté scientifique. Du fait qu'un grand nombre de modèles sont actuellement employés pour l'évaluation des risques liés à différents groupes d'espèces, la nécessité de disposer de systèmes validés sur le plan biologique se fait sentir. Ces dernières années, des progrès ont été réalisés dans la recherche sur les caractéristiques des espèces et des habitats contribuant au risque d'invasion biologique. Les modèles validés atteignent aujourd'hui une précision pouvant aller jusqu'à 85%. Lors de l'introduction d'un petit nombre d'individus, la dynamique des populations dépend des conditions locales. C’est pourquoi de nombreux experts sont d’avis qu’il est quasiment impossible d’effectuer des prévisions plus précises à l’égard du risque d’invasion. L’exactitude requise des modèles dépend en grande partie de l’importance des pertes économiques entraînées par l’interdiction de l’introduction d’un organisme désigné à tort comme envahissant. Il n’est pas possible de prévoir exactement quelles espèces deviendront envahissantes parmi les innombrables organismes non indigènes importés par l’homme, volontairement ou non, dans de nouvelles régions. Toutefois, les modèles peuvent fournir des indications précieuses sur le pouvoir envahissant d’organismes non indigènes ou transgéniques. Les organismes présentant un risque accru pourront ainsi être surveillés et étudiés de manière plus approfondie (voir les études de cas au chapitre 6).

Riassunto

Introduzione

La diffusione di organismi non indigeni o alieni ha raggiunto proporzioni di gran lunga superiori a quelle che ci si potrebbe attendere nell'ambito di un processo naturale. Alcune di queste specie hanno ampiamente colonizzato i loro nuovi territori e causano notevoli danni economici ed ecologici. In ogni caso, va sottolineato che soltanto una piccola parte delle specie introdotte in una regione nuova si trasforma in invasiva. Circa il 10% di tutte le specie trasportate involontariamente giunge in un nuovo territorio. Solo il 10% di tale percentuale riesce però ad insediarvisi con successo e di queste specie insediate soltanto il 10% circa diventa, a sua volta, invasivo. Ciò significa che circa una specie su mille importata causa problemi ecologici o economici. Di fronte allo scenario appena illustrato, diventa di centrale importanza saper prevedere quali sono le specie aliene che riusciranno a sopravvivere o addirittura a diventare invasive. La possibilità di fare delle previsioni precise al riguardo ci permetterebbe di evitare notevoli danni ecologici ed economici.

Le invasioni biologiche avvengono in genere in quattro tappe: a) importazione, b) emissione nell'ambiente, c) insediamento e d) invasione nel senso stretto del termine. La bibliografia è ricca di informazioni sulle caratteristiche delle specie correlate ad un incrementato rischio di un'invasione efficace sul ruolo importante svolto dalle condizioni in cui avviene la loro introduzione nei rispettivi habitat. In questi ultimi anni sono stati compiuti considerevoli progressi anche per quanto riguarda l'identificazione delle caratteristiche di un habitat che incrementano il pericolo d'invasione. Il presente studio bibliografico riassume le informazioni attualmente disponibili.

Il primo capitolo elenca gli obiettivi e descrive la metodologia dello studio. Il secondo capitolo esamina le caratteristiche di un habitat che favoriscono il pericolo d'invasione. I capitoli seguenti si occupano delle caratteristiche che incrementano il rischio d'insediamento (capitolo 3) o di diffusione (capitolo 4) di una specie. Il capitolo 5 presenta invece modelli che tentano di dare una spiegazione a invasioni ormai già avvenute o di predire in maniera possibilmente esatta il rischio di future invasioni. Il capitolo 6 contiene infine tre casi esemplari sulla valutazione dei rischi legati ad organismi scelti, volti ad illustrare alcuni aspetti importanti di una buona ricerca in materia di rischi.

La maggioranza degli studi pubblicati sinora sulle caratteristiche delle specie e degli habitat connessi ad un maggiore potenziale d'invasione è stata effettuata fuori dai confini dell'Europa. Il presente studio tenta di stabilire in che misura le conclusioni tratte sono valide anche per il nostro continente. Inoltre, discute dell'importanza dei risultati emersi dalle ricerche condotte su organismi esotici ai fini dell'analisi dei rischi connessi ad organismi transgenici.

Caratteristiche degli habitat

La maggioranza degli studi sui fattori che rendono un habitat più o meno vulnerabile alle invasioni è stata eseguita esaminando delle piante invasive. In tal ambito, è stata identificata una serie di caratteristiche tipiche di un habitat correlata ad una maggiore predisposizione a subire invasioni biologiche. L'esempio evidenziato dagli studi elencati nell'appendice 1 lascia supporre che una maggiore disponibilità di risorse, sia per influsso sia per una modifica del regime di disturbo, incrementi il pericolo d'invasione da parte di piante esotiche, dato che la sopravvivenza di una pianta è, in primo luogo, legata alla disponibilità delle necessarie risorse.

Sono pochi gli studi che hanno cercato dei fattori intrinseci agli habitat che aumentano il rischio di un'invasione da parte di specie fungine o animali.

Allo stato attuale della ricerca non è quindi possibile identificare i fattori rilevanti ai fini di un'invasione da parte di tali organismi. Indicazioni al riguardo sono giunte da progetti sul controllo biologico dei parassiti, i quali mostrano che i predatori indigeni svolgono un ruolo importante nell'insediamento di erbivori esotici.

Caratteristiche delle specie

Esiste una serie di caratteristiche di una specie correlata all'insediamento dalla successiva diffusione o proliferazione della stessa. L'insediamento duraturo è favorito da caratteristiche che permettono ad una popolazione di raggiungere una densità talmente alta da ridurre ai minimi termini il pericolo di estinzione (ad es. in base a processi stocastici). Dette caratteristiche includono fra l'altro il sistema di riproduzione (ad es. la riproduzione asessuale), il numero di discendenti o la durata dello stadio giovanile (appendice 3). Per contro, vi sono caratteristiche che si ripercuotono sugli effettivi della popolazione (ovvero la quantità di individui che si riproducono) e sono correlate negativamente con l'insediamento, come ad esempio la selezione sessuale degli animali o i sistemi di fecondazione complessi.

Singoli studi lasciano invece supporre che il meccanismo di diffusione delle specie esotiche costituisca l'indicatore di un maggiore rischio di proliferazione. Una pronunciata tendenza alla proliferazione e alla diffusione è da attendersi anche quando specie già insediatesi con successo modificano in maniera duratura le condizioni vigenti in un habitat. Recentemente sono stati pubblicati diversi studi che stabiliscono un rapporto fra l'invasione dell'America del Nord da parte di specie vegetali esotiche e secrezioni radicali di sostanze allelopatiche, che esulano dall'esperienza della flora indigena. L'importanza della variabilità genetica nell'ambito dell'invasione di nuovi habitat da parte di specie già insediatesi con successo non può ancora essere valutata in maniera conclusiva. Va però ricordato che alcune specie vegetali invasive sono nate dall'ibridazione di diverse specie o di varie popolazioni della stessa specie.

Alcuni fattori che non costituiscono delle vere e proprie caratteristiche delle specie sono considerati ottimi indicatori del potenziale invasivo di una specie. Il migliore indicatore di pericolo relativo ad un insediamento efficace e a una proliferazione massiccia di una specie è costituito probabilmente dalla risposta alla domanda se la specie interessata o altre specie della stessa famiglia siano già diventate invasive in altre regioni del pianeta. Inoltre, sono ripetutamente menzionate l'estensione e la situazione geografica del territorio naturale di diffusione (appendice 3). Molto importanti per l'insediamento efficace di una specie sono inoltre anche la quantità delle importazioni e il numero di individui diffusi nell'ambiente.

Modelli per valutare il rischio d'invasione

Diversi studi hanno tentato, più o meno con successo, di spiegare in retrospettiva e utilizzando le caratteristiche specifiche delle specie, quali specie sono riuscite a insediarsi e a diffondersi fuori dal loro habitat di naturale e per quale motivo vi sono riuscite. Insieme a tali studi sono stati elaborati anche dei modelli per valutare la probabilità di possibili invasioni. Dato che la responsabilità dell'invasione di diversi gruppi di organismi sembra poter essere attribuita a fattori diversi, simili modelli vengono in genere sviluppati per gruppi di specie limitati dal punto di vista tassonomico, per esempio le specie vegetali o l'avifauna.

I modelli sviluppati si basano su dati qualitativi o quantitativi concernenti la storia della diffusione di una specie o di specie imparentate, nonché su caratteristiche considerate rilevanti per le specie esaminate dal punto di vista del loro potenziale invasivo. Nonostante tali modelli siano oggi in parte già utilizzati dalle autorità, soltanto alcuni di essi sono già stati esaminati dal profilo della loro attendibilità. Il problema di fondo legato alla valutazione del potenziale invasivo di nuove specie è che sono poche quelle che diventano invasive. Ne consegue che persino un modello con un grado di precisione dell'85% implica che un notevole numero di specie venga erroneamente catalogato come invasivo, quando in realtà esse non comportano alcun rischio in tal senso. Ciò può avere delle conseguenze negative, in particolare quando il divieto d'importazione di una specie considerata erroneamente invasiva è legata a grosse perdite economiche.

Conclusioni

Fare delle previsioni precise sulla probabilità che una specie diventi invasiva rimane e rimarrà una grande sfida scientifica. L'applicazione, nella prassi vigente, di un notevole numero di modelli di valutazione dei rischi intrinseci a diversi gruppi di specie indica che esiste un bisogno di sistemi valicati dal punto di vista biologico. In questi ultimi anni, la ricerca di caratteristiche delle specie e degli habitat che comportano un aumento dei rischi d'invasione biologica ha compiuto progressi. Le previsioni scaturite dai modelli esaminati raggiungono oggi un grado di precisione che arriva sino all'85%. Dato che la dinamica di piccole popolazioni rilasciate deliberatamente nell’ambiente dipende dalla condizioni locali, numerosi esperti sono oggi del parere che sia praticamente impossibile fare delle previsioni di carattere generale sulle invasioni. La precisione dei modelli dipende in gran parte dall’entità delle perdite economiche causate dal divieto d’emissione di organismi ritenuti erroneamente invasivi. Nonostante sia impossibile determinare con precisione quali delle numerose specie non indigene o aliene, introdotte consapevolmente o inconsapevolmente dall’uomo in una nuova regione, diventeranno o non diventeranno invasive, i modelli di previsione possono per lo meno indicare quali organismi esotici o transgenici possiedono un potenziale invasivo superiore e devono quindi essere studiati (cfr. esempi nel capitolo 6) oppure osservati con maggiore attenzione.

Summary

Introduction

As a result of human activities the spread of non-indigenous or “alien” organisms has today reached a scale that is well beyond what could be expected from natural processes. Some of these species have extensively colonised their new homes, causing great economic and ecological losses. It should however be noted that only a small portion of the species introduced into a new region become invasive: about 10 per cent of all displaced species are released into the new territory, 10 per cent of these succeed in establishing themselves, and a further 10 per cent or so of the established species become invasive. In other words only something like 1 per 1000 displaced species result in ecological or economic problems. The big question in this context is whether or not it is possible to predict which non-native species are likely to establish themselves and in particular which will become invasive. If it were possible to make relatively accurate predictions in this sense, major ecological and economic losses could be avoided.

Biological invasions generally have four phases: a) importation, b) naturalization, c) establishment d) and invasion in the strictest sense of the word. The literature provides abundant information on species characteristics that are correlated with the increased risk of a successful invasion, and about the importance of the introduction methods. In recent years considerable progress has been made in the identification of habitat characteristics that increase the danger of an invasion. This study of the literature brings together the information available at present.

Chapter 1 describes both the objectives of the study and the methodology. Chapter 2 deals with the kind of habitat characteristics that increase the risk of an invasion. The subsequent chapters discuss the species characteristics that increase the risk of establishment (Chapter 3) and of population build-up and spread (Chapter 4). Chapter 5 deals with the predictive systems or models that either attempt to throw light on invasions that have already taken place or attempt to predict as accurately as possible the risk of future invasions. Finally in Chapter 6 I present three case studies assessing the level of risk attached to given organisms, intended to demonstrate the most important aspects of good risk research.

Most of the studies that have been published on species and habitat characteristics that are associated with an increased invasion potential have been conducted outside Europe. The present study attempts to establish to what extent the conclusions reached by these studies also apply to Europe. The significance of the collected findings from research into exotic organisms for analysis of the risks attached to transgenic organisms is also discussed.

Habitat characteristics

Most of the studies of factors that make a habitat more or less susceptible to invasions have concentrated on invasive plants. These studies have identified a whole series of habitat characteristics correlated with increased susceptibility to biological invasions. As can be seen from the sample provided by the studies listed in Appendix 1, it appears that an increase in the availability of resources, be it from the influx of resources or an alteration in the disturbance regime, increases the danger of invasions by exotic plant species, since plants are primarily resource-limited.

Only a few studies are based on research into the habitat factors which increase the risk of an invasion by mushrooms or animals. It is therefore not possible at the present stage to identify the factors relevant to invasions by such organisms. However the evidence of certain biological pest control projects indicates that domestic predators play an important role in the establishment of exotic herbivores.

Species characteristics

There is a whole series of characteristics that correlate with successful establishment and subsequent build-up and/or spread. Thus lasting establishment is favoured by characteristics that enable a population to reach such a density that the danger of extinction (for example due to stochastic processes) is minimised. Among other things these characteristics include the reproductive system (e.g. asexual reproduction), the number of offspring and the length of the juvenile period (Appendix 3). On the other hand there are characteristics that reduce the effective population size (i.e. the number of reproductive individuals), and are negatively correlated with successful establishment, examples being sexual selection among animals and complex pollination systems.

Certain studies suggest that the dispersal mechanism of established exotic species is an indicator for an increased risk of proliferation. One must in any case expect an increased tendency to propagate and reproduce when established species cause lasting changes in the habitat conditions. According to a number of studies published in recent years, the successful invasion by exotic plant species in North America had to do with allelopathic root exudates, with which domestic flora had no experience. The importance of genetic variability in the propagation and the colonisation of new habitats by established species cannot yet be assessed in any conclusive manner. It is worth noting however that some invasive plant types have emerged from the hybridisation of a variety of species or from a variety of populations of the same species.

A number of factors that are not species characteristics in the true sense of the word nonetheless serve as good indicators of a species' potential as an invader. The best indicator of increased danger of a successful establishment and proliferation seems to be whether or not the species in question, or other species of the same genus, have already shown themselves to be invasive in another region of the world. Furthermore the size and the geographical position of the natural propagation area are once again taken into consideration (Appendix 3). The number of imports as well as the number of individuals released is also of great importance for successful establishment.

Models for assessing the risk of invasions

Various studies based on species characteristics have attempted to show retrospectively, with more or less success, what species have managed to establish themselves and spread beyond their natural propagation area, and why. In addition to these retrospective studies, predictive systems or "models" have been developed to assess the probability of the invasions viewed as possible. Since various factors seem to be responsible for an invasion by different groups of organisms, such models are usually developed for taxonomically limited species groups, such as for example plants or birds.

The models that have been developed are based either on qualitative or quantitative data concerning the history of the propagation of a species or related species as well as on the species characteristics which are considered relevant to their potential as an invader in the case of the species under investigation. Although these models are already used to some extent by the authorities today, only a few have been tested as to their accuracy. The basic problem in accurately predicting the invasive potential of new species is that only very few of the imported species actually become invasive. Thus even with a model that has an accuracy of 85 per cent a large number of species are erroneously categorised as invasive which in fact involve no such risk. This can have particularly negative consequences when a ban on the import of a species erroneously considered as invasive leads to major economic losses.

Conclusions

Accurately predicting the probability of a species becoming or not becoming invasive remains one of the great challenges facing science. The fact that a great many risk assessment models are in use today for a variety of species groups is an indication of the need for biologically validated systems. Progress has been made in recent years in the search for the relevant species and habitat characteristics that increase the risk of biological invasion. The quality of tested models today has a forecasting accuracy of up to 85 per cent. Since the population dynamics of small released populations depends in each case on local conditions, it is the view of many experts that accurate general predictions of invasions are scarcely possible. How accurate such models must be depends to a great extent on how great would be the loss to the economy resulting from a ban on the introduction of organisms erroneously classified as invasive. Even if it will never be possible to accurately predict which of the many non-indigenous species that are knowingly or unknowingly introduced to a new region will become invasive and which not, forecasting models can nonetheless at least provide valuable indications as to which exotic or transgenic organisms exhibit an increased invasive potential and should therefore be studied or observed more closely (see case histories in Chapter 6).

Introduction

The biota of the earth are currently experiencing a dramatic transformation. The structure and functioning of most ecosystems have been and are being altered by the activities of humankind. In parallel, humans are purposefully and inadvertently moving biological material across natural barriers leading to mixing of formerly separated species assemblages, a process which is essentially irreversible. Historical fluctuations in climate and biota have led some to say that nothing new is happening that has not already happened before. This is indeed true, but the rate of biological invasions today exceeds anything in the past (Wittenberg and Cock 2001). Biological invasions are the uncontrolled spread and proliferation of species or genotypes to areas outside their native range. Before the age of Exploration, dispersal of organisms across biogeographic barriers was a low-probability event; today this is routine, and as the volume of global trade and tourism increases, it is likely that the rate of establishment of alien species will also increase.

Invasive alien (exotic) species are serious threats to natural, agricultural and urban ecosystems. The ecological impact of invasive alien species is particularly evident on isolated islands, where invasive alien species are the single most important factor for species extinctions (Wilcove *et al.*. 1998). Also, biota on continents colonized by emigrants from Europe and Asia in the 18th and 19th century are particularly threatened by invasive alien species (e.g. North America, South Africa, Australia, New Zealand). Besides species extinction, potential ecological impacts by invasive alien species include displacement of individual species or species assemblages (Richardson *et al.* 1989, Porter and Savignano 1990, Stohlgren *et al.*. 1999), genetic pollution of local populations by hybridisation (McMillan and Wilcove 1994), alteration of abiotic factors (Vitousek and Walker 1989) and of ecosystem processes (Williams and Baruch 2000). Invasive alien species can also cause enormous economic losses; a recent analysis for North America estimated an annual loss of approximately 137 billions of US Dollars (Pimentel *et al.*. 2000). The addition of any novel organism in new areas also creates opportunities for evolution, making predictions of impacts even more difficult (Mooney and Cleland 2001).

In Europe, both the current damage inflicted by invasive alien species as well as public perception of the risks of invasive alien species are lower than in regions listed above. Whether invasive species will ever have the same devastating effects as they already have in North America or New Zealand is debateable. There are indications that the European habitats are less susceptible to invasion by exotic species than habitats in other parts of the world (see chapter 2), but the relatively moderate damage inflicted by invasive alien species in Europe so far may also be due to a relatively early stage during the invasion process. There can be a long period between an introduction and the spread of an invader, and little is known about what determines the length of this early phase of invasion, which is called 'lag phase' (Kowarik 1995a). In any case, the fact that exotic species have already invaded – and are still invading – Europe leaves no doubt that European habitats are also invasible. Examples of exotic species in Europe with documented ecological and/or economic impacts include corn root-borer, *Diabrotica virgifera* (Krysan and Miller 1986), ragweed, *Ambrosia artemisifolia* (Déchamp 1995), argentine ants

(Tsutsui *et al.*. 2001), and the alga *Caulerpa taxifolia* in the Mediterranean Sea (Meinesz 1999).

Only a few of the many non-indigenous species that arrive in an area become invasive. Williamson and Fitter (1996) summarized the fate of introductions in a rule of thumb known as the 'tens rule'. This rule defines the stages of introduction as (i) importation, (ii) naturalization, (iii) establishment, and (iv) invasion. The tens rule states that roughly 10% of the species imported will make the transition from one stage to the next. Hence, it predicts that approximately 0.1% of all species imported to an area will eventually become pests.

A key question in this regard is whether it is possible to predict which non-indigenous species would be able to establish and become invasive. If accurate predictions of invasiveness could be made, enormous costs could be saved. One concern brought up by some is that only a minority of species that are introduced to a new range are deliberately released, and are therefore subject to a risk assessment. However, the majority of weedy aliens were deliberately introduced: some 50% of the major weeds in Australia have been introduced purposefully, while only 18% are known to have been introduced accidentally. Similarly, at least 82% of the woody species that are invasive in the United States of America were introduced for horticulture (Reichard 1997). However, a different picture may emerge when analysing other organism groups, such as insects or pathogens.

In recent publications, the four transitions in the invasion process mentioned above are examined separately. Because several factors determine the probability that a species will complete each transition successfully, it is probable that the species characteristics important in completing different transitions will also be different. It has been suggested that early reviews did not detect patterns in species characteristics across studies because they examined all transitions together (Kolar and Lodge 2001).

The literature on invasion ecology provides a great deal of information on the characteristics of an organism that may contribute to increased risk of invasiveness, and to a more limited extent on the importance of introduction methods. In the past two decades, considerable progress has been made in identifying habitat traits that enhance the risk of habitat invasibility. Since the habitat 'sets the stage' in which invasion processes take place, such habitat traits affecting invasion will be reviewed in this study as well.

Aim of the study

The main objectives of this literature review were to:

- Identify and analyse the characteristics of exotic and/or transgenic organisms that contribute to their potential invasiveness;

- Determine extrinsic factors, such as biotic and abiotic characteristics of potentially affected habitats, that could allow non-indigenous species to become invaders;
- Quantitatively evaluate the explanatory power of factors that are linked to exotic species becoming invasive;
- Assess the extent to which these factors can be used in a prediction system that generates statements about the likelihood that events will occur, and to
- Review approaches that have been applied to assess the potential invasiveness of specific exotic or transgenic species or genotypes.

Information on the first two steps in the invasion process, namely importation and naturalization, will not be discussed in detail in this study, since survival of species largely depends on the pathways of introduction and the handling of the organisms in the new range. It is though worthwhile to keep in mind that most alien weeds were originally introduced intentionally, and may therefore have been selected according to some specific traits that also enhance the invasiveness (e.g. ability to stabilize soil).

Emphasis has been put on distinguishing between purely retrospective studies and studies that also include a predictive approach; the former aim to explain why some species have become invasive and others not, while the latter try to make statements about the likelihood that a particular non-indigenous species will become invasive. Retrospective studies include i) multi-species studies that statistically assess what traits are correlated with increased invasiveness, or ii) experimental studies in which life-history traits of a few closely related invasive and non-invasive species are compared. Predictive tools include c) multi-species studies that test how well a model developed in a retrospective study predicts the risk of invasiveness in a separate set of species, d) qualitative risk assessment systems, and e) experimental or modelling case studies that try to assess the risk of invasiveness before an organism has been released into the environment.

Significance of the progress in invasion biology for the risk assessment of genetically modified organisms

Explaining and predicting the likelihood of increased invasiveness is not only important with regard to exotic organisms, but also with regard to genetically modified organisms (GMOs). Risks associated with GMOs and invasiveness are twofold: the most publicized risk is the evolution of increased weediness as a result of the sexual transfer of new alleles to wild relatives. Spontaneous hybridisation between crops and their wild relatives has already led to the evolution of difficult weeds, such as weed beets in Europe (Boudry *et al.*. 1993, Mücher *et al.*. 2000) and weed rye in California (Suneson *et al.*. 1969, Sun and Corke 1992). The transgenic plant itself may also become an environmental problem if the transgenic trait(s) it expresses alters its ecological performance such that it becomes an invasive species or economic weed. For some crops, weedy and/or wild populations often grow in close association with the cultivated forms of the same species. For example, Pessel *et al.* (2001) confirmed that feral oilseed rape plants growing on road verges do not originate from the current or previous year's cultivation of the crop. In fact, they showed that the relict plants represent a cultivar type of oilseed rape no longer sold, which has persisted in a semi-natural habitat for at least 8 years. The existence of such populations suggests that if GMOs confer the ability to overcome factors that limit wild populations, the resultant genotype might be even more weedy or invasive than its non-transgenic progenitor. This review tries to elucidate whether and how the knowledge gained during 40 years of invasion ecology research may help in improving the risk assessment of increased invasiveness by GMOs outside the crop field.

Implication for Switzerland and Europe

Most of the currently available evidence is based on research carried out in Australia, New Zealand, North America and South Africa. As far as possible, emphasis will therefore be put on assessing whether the conclusions that can be drawn from current evidence are also valid in a Swiss or European context.

Methods and material

A literature review was carried out by screening the electronic databases for publications on:

- quantitative studies which investigated patterns between life-history traits and predisposition for increased invasiveness
- studies which assessed the importance of extrinsic (habitat, climate) factors, either alone or in combination with species' traits, in predicting increased probability of invasion
- case studies which aimed to elucidate life-history traits that explain increased invasiveness of selected Invasive alien species or genetically modified organisms

The following electronic databases were screened: CAB Abstracts, CSA, Web of Science, Agricola, JStor, Bioagindex). Keywords used in the search included invas*, invad*, exotic, alien, nonindigenous, invasion ecology, biological invasions, invasiveness, transgenics, and combinations thereof. In addition, requests were made to colleagues working in this field for unpublished material. The review generated some 300 relevant references, which were put in an 'Endnote' file.

From these publications, information was collated on the:

- intrinsic and extrinsic factors that (at least partially) explain increased invasiveness,
- experimental and statistical approaches used to identify patterns,
- explanatory power of these retrospective studies,
- designs of predictive risk assessment systems that are at least partly based on species traits, and the
- explanatory power of these predictive systems

Outline of the report

This review first presents an overview of habitat characteristics that have been shown in comparative or experimental studies to correlate with increased risk of habitat invasibility (chapter 2). Chapters 3 and 4 will then summarize the species traits that increase the likelihood that a species will successfully complete the two final transitions in the invasion process mentioned above. Chapter 3 focuses on establishment, and chapter 4 on the population build-up and spread in the new habitat. The information discussed in chapters 3 and 4 are primarily collated from multi-species comparisons that tried to assess retrospectively whether certain species traits increase the likelihood of successful completion of a transition. The information compiled in chapters 2-4 has been used in developing qualitative and quantitative predictive systems, of which several will be presented in chapter 5. Chapter 6 provides short summaries of selected case studies to illustrate best practise of how to assess the potential risk of increased invasiveness by exotic species or GMOs. The final chapter tries to draw some general conclusions from the previous chapters, and to make some suggestions as to how our current knowledge of invasion processes may be further improved, and how it can be applied to improve our ability to predict the degree of invasiveness of exotic or transgenic organisms.

Often, no clear distinction is made between factors that facilitate the establishment of exotic organisms and those that favor subsequent invasion. In order to make direct comparisons of species traits that increase likelihood of invasiveness (chapters 3 and 4), the literature has been sorted with regard to whether habitat characteristics have been tested for their role in increased risk of establishment (third phase in the invasion process), or for their role in the actual invasion step (population build-up and local spread). Since many studies did not explicitly distinguish between these two steps in the invasion process, the findings were arbitrarily attributed to one of the two steps as follows: studies in which the number of exotic (sometimes also non-sown native) species in a habitat or the number of successfully establishing offspring from one or several species were measured are considered to assess the risk of successful establishment of invasive species. Studies in which cover, relative growth rate or population growth rate of non-indigenous species were recorded are considered to test for population build-up and/or spread (Appendix 3).

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1 Invasibility of habitats

The concept of 'environmental resistance' (Chapman 1931) was introduced to describe the forces, primarily biotic, that hinder the establishment of species in a new location. In the past decades, evidence has accumulated that invasion processes depend to a large extent on the characteristics of the potentially threatened habitats, and particularly upon the interaction between the characteristics of non-native species and their potential new habitats. In this chapter, an overview will be given of habitat characteristics that have been shown in correlative or experimental studies to be positively or negatively correlated with the probability of successful establishment or invasion by non-indigenous species, and how they interact with species traits.

The majority of studies investigating habitat invasibility have been carried out with regard to the risk of invasion by exotic plant species. Much less information is available on habitat characteristics that increase the risk of invasion by animals.

1.1 Factors affecting habitat invasibility

At least five interacting factors have been invoked to account for differences in invasibility: evolutionary history, community structure, propagule pressure, disturbance and abiotic stress (Alpert *et al.* 2000).

1.1.1 Evolutionary history

Aspects that are thought to affect the invasibility of habitats include past intensities of competition and of human disturbance. Oceanic islands, for example, are considered to be habitats with relaxed selection for competitive ability, which may explain their highly vulnerability to invasion (Loope and Mueller-Dombois 1989). Habitats with a long history of human disturbance may have lower invasibility because their native species have already been selected to perform well under disturbed conditions, or because open niches had already been filled by exotic species, which are now called archaeophytes, thousands of years ago (di Castri *et al.* 1990).

Communities which experience new forms of interactions with which they have had no evolutionary past may be particularly susceptible to biological invasions. For example, the North American prairies have evolved under limited grazing pressure by large mammals. The introduction of cattle and the resultant high grazing pressure has facilitated the invasion by exotic plant species that have evolved in areas with large mammals, and are physically or chemically adapted to grazing by large mammals (Mack 1989).

1.1.2 Propagule pressure

As will be outlined in chapter 3, establishment success largely depends on the number of individuals released into a specific habitat. Propagule pressure can also be habitat-specific. For example, propagule pressure might tend to be less in more stressful habitats, such as desert or high mountain habitats, because they are less frequented by people. Furthermore, fragmented, small habitats are exposed to higher propagule pressure from surrounding, usually disturbed habitats.

1.1.3 Resident community structure

Features of community structure that have been put forward to influence invasibility include species richness, functional group richness, the strength of interactions between species, and assemblages of natural antagonists. In theory, more diverse communities might use resources more completely and reduce their availability to potential invaders (Tilman 1997). Therefore, more diverse communities should be less invasible. Such a pattern has indeed been found in experimental studies in which communities with manipulated numbers of species richness were tested for their invasibility (Appendix 1). However, a number of correlative field studies found no or even positive correlations between native species richness and degree of invasion (e.g., Stohlgren *et al.* 1999). This apparent contradiction has led to controversy in the literature. Levine *et al.* (2002) suggest a framework that resolves these different results by distinguishing the local or causal effects of diversity from the factors associated with diversity across communities. According to their framework, experimental manipulations of diversity examine the intrinsic or causal effects of diversity on invasion resistance. In contrast, the correlations between diversity and invasion resistance across entire communities result from these effects, but also the effects of factors covarying with diversity across natural systems. The covarying factors are those known to influence native diversity, such as disturbance, resource availability, and propagule supply.

However, whether the pattern found in experimental studies indeed demonstrate that there is a causal effect of diversity on invasion resistance remains a matter of debate. Wardle (2001) proposes another explanation for the apparent discrepancy between the results of correlative and experimental studies. In correlative studies, competitive dominant species are often associated with the most productive plots, and these dominants both reduce diversity through competitive exclusion of native subordinates and competitively suppress invasive species. Furthermore, in experimental studies ‘sampling effects’ result in the most competitive species occurring with greater frequency as diversity is increased. According to this explanation, both correlative and experimental studies would point to a role for competitive dominants in reducing invasibility, and species richness per se of the plant community need not be invoked as an explanation for the results.

The ‘enemy release hypothesis’ has been put forward to explain the increased invasibility of non-native species (Keane and Crawley 2002). This hypothesis states that plant species, on introduction to an exotic range, should experience a decrease in regulation by natural enemies, resulting in an increase in distribution and abundance. Numerous studies have documented a reduced enemy richness in the exotic range, resulting in a reduced overall herbivore pressure (reviewed by Keane and Crawley 2002; Mitchell and Power 2003, Torchin *et al.* 2003, but see Agrawal and

Kotanen 2003).The success of classical biological control has been used as support for the enemy release hypothesis, but Keane and Crawley (2002) emphasize that the success of classical biological weed control, although showing that introduced enemies can regulate invasive exotic plants, does not provide clear evidence that enemy release plays a central part in the invasion success of exotic species. At a smaller scale, fragmented habitats that lack species from higher trophic levels have been shown to be more vulnerable to invasion by members of lower trophic levels (Kruess and Tscharntke 1994).

Conversely, positive interactions between the invaders and native symbionts, such as mycorrhizal fungi (Marler *et al* 1999), nitrogen-fixing bacteria (Vitousek *et al.* 1987) or pollinators (Richardson *et al.*, 2000) may increase invasibility.

Recent studies on soil-plant interactions have stimulated discussion on the role of soil microorganisms in habitat invasibility. For example, Klironomos (2002) showed that invasive species tend to lack negative plant-soil-plant feedbacks that seem to be common in the population dynamics of native plant species. Klironomos (2002) provided evidence that it was a lack of negative interactions between pathogenic soil microorganisms and the invasive species that may be responsible for the observed patterns. Callaway and Aschehoug (2000) showed that invaders have a higher competitive ability when growing with new neighbor plants from the exotic range than with their old neighbors from the native range. On sterile soil, these differences disappeared, indicating that microorganisms are responsible for the increased competitive ability of the invader in the new range. It is likely that investigations on the effect of soil micro- and macro-organisms on vegetation composition and succession will significantly advance our understanding of plant invasion processes.

Some of the habitat characteristics listed in Appendix 1, such as resource availability, seem to play a central role in invasion by exotic plant species, but have not been identified as a driving factor in invasion processes of herbivorous or predatory animals. Whether this pattern reflects a biased research activity, or whether indeed distinct sets of characteristics make habitats more or less invasible for organisms of higher trophic levels remains to be shown. Hairston *et al.* (1960) posit that certain trophic levels in a food-web are more likely to invade habitats than others. According to their hypothesis, competition will be intense for plants, carnivores and decomposers because they are resource-limited, but relatively unimportant for herbivores, since these are kept scarce in relation to their resources by the action of natural enemies. In a review of biological weed control programmes, native predators accounted for 22% of all failures to successfully establish exotic biocontrol agents, parasitoids for 11% and diseases for 8% (Crawley 1986). Competition with native herbivores was recorded to be the cause for failure in 12% of all release attempts. Crawley (1986) concludes that the presence of high densities of resident, generalist natural enemies can be just as potent a force in resisting (deliberate) invasion by biocontrol agents as the presence of competitors.

Invasion success may also depend on the presence or absence of other exotic species in the new range. Exotic species may interfere with each other in the new range, but often they facilitate each other's establishment and spread. For example, in Ireland the shrub *Rhododendron ponticum* causes considerable ecological damage to the recipient woody habitat. Originally, the shrub profited from heavy disturbances due to logging activities by humans. The introduction of the Japanese sika deer (*Cervus nippon*) in 1860 initiated a new form of woodland disturbance: *R. ponticum* becomes established on bryophyte covered patches created when the sika deer overgraze (Cross 1981). Such synergistic interactions among invaders, a process termed 'invasional meltdown', is considered to lead to accelerated impact on native ecosystems (Simberloff and Von Holle 1999).

1.1.4 Disturbance

Disturbance can be defined as a punctuated event that kills organisms or removes part of their biomass (D'Antonio *et al*. 2001). Numerous studies have shown that disturbance, such as grazing or fire, can strongly affect habitat invasibility; in fact, disturbance, or strictly speaking a change in the traditional disturbance regime, is considered to be one of the key factors affecting habitat invasibility. However, as shown below, the risk of invasion of disturbed habitats appears to depend on the level of abiotic stress, such as low resource availability, acting on the exotic species in the new habitat (Alpert *et al*. 2000). Long-term disturbance regimes may allow local species to adapt to the conditions imposed by the typical regime (see also 'Evolutionary history' above). It is therefore primarily new disturbances in formerly undisturbed habitats and changes in the typical disturbance regime that are believed to increase the risk of invasibility.

1.1.5 Abiotic stress

Three types of abiotic stress have been hypothesized to affect invasibility: low resource availability, environmental conditions that limit plant growth such as extreme temperature, and presence of toxins. Tests of the hypothesis that stress affects invasibility include comparisons between habitats with different stress levels, experimental manipulations of stress in the field, and comparisons between the abilities of invasive vs. native species to tolerate, perform or compete at different resource levels.

In general, adding nutrients to a habitat raises invasibility. Experiments in which co-occurring native and non-native plants were grown separately or in mixtures consistently showed that the invasive species grow more quickly than the natives at high soil nutrient conditions. Low soil nutrient availability can diminish the relative competitive advantage of non-native species, or even reverse the outcome of competition (Burke and Grime 1996; Wedin and Tilman 1993). Invasion by exotic plants may not be restricted to habitats with constantly increased resource availability; short-term nutrient flushes may be enough to make a habitat more invasible (Davis *et al*. 2000).

Results from experiments in which both resource availability and disturbance were manipulated suggest that the effect of resource availability on invasion depends on changes in disturbance regime (Davis and Pelsor 2001). Alpert *et al.* (2000) propose a model for interactive effects of stress (such as nutrient availability) and disturbance on habitat invasibility (Fig. 1); according to their model, habitats should be invasible when stress is very low, when disturbance is greatly increased or decreased, or when relatively low stress is combined with relatively large departures from typical disturbance regimes.

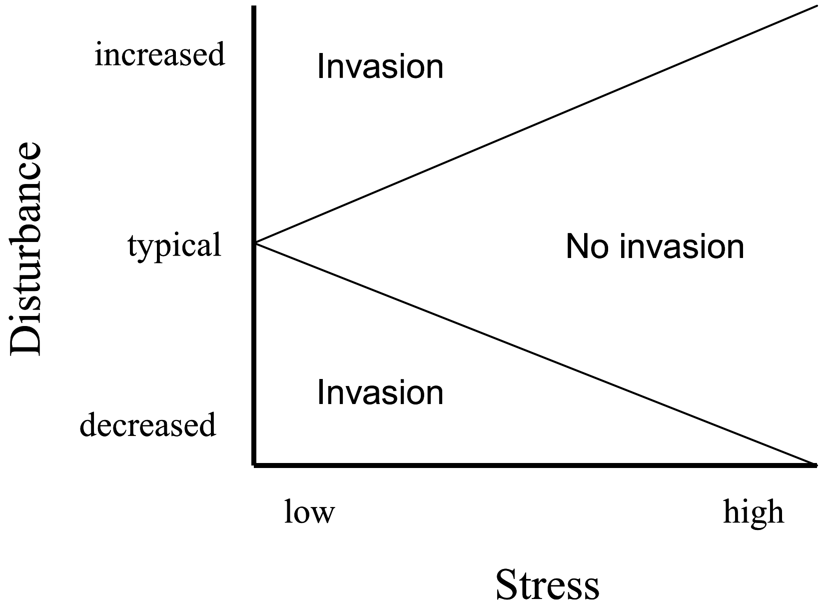

Figure 1. Model for interactive effects of abiotic stress and disturbance on habitat invasibility (Alpert *et al.* 2000).

1.2 Invasibility of European habitats

There is evidence that habitat invasibility in Europe is triggered by similar factors as in other parts of the world. For example, studies carried out in Europe indicate that change in disturbance (Thompson *et al.* 2001), resource availability (Davis and Pelsor 2001) presence of antagonists (Prieur-Richard *et al.* 2001) and species richness of the resident community (van der Putten *et al.* 2000) are correlated with risk of invasibility of European habitats (see also Appendix 1). It should be noted, though, that numerous studies on habitat invasibility carried out in Europe have used native weedy species as surrogate species for alien invasive species. One of the exceptions is a study by Kowarik (1995b) in which a highly significant correlation was found between the average anthropogenic disturbance and the percent exotic species established in different habitats in the surrounding of Berlin, Germany.

An important but unresolved question is whether the overall invasibility of European habitats is comparable to those of other continents. This question is primarily discussed in the context of invasions by exotic plant species. As already mentioned in the introduction, rapid invasions by exotic animals and pathogens has repeatedly occurred in Europe, and are without any doubts continuing to take place in the future. The European plant species, on the other hand, have a longer history of intensive human disturbance than plant species in many other parts of the world, e.g. in the prairies of North America or on oceanic islands. It has therefore been suggested that native European vegetation is well adapted to (changes in) disturbance, one of the key factors correlating with increased risk of habitat invasibility (Appendix 1). However, the fact that numerous exotic plant species have now reached the log-phase in their invasion process in Europe (Kowarik 2003) clearly underpin that European habitats are by no means prone against invasions by exotic plant species.

1.3 Summary

The pattern emerging from the studies listed in Appendix 1 suggests that plants are primarily resource limited, and that an increase in resource availability through resource addition or change in competition due to an altered disturbance regime facilitates establishment and spread of exotic plant species, as they are generally better adapted to transform increased nutrient availability to biomass.

A potentially important but still largely under-investigated habitat characteristic is the effect of soil micro- and macro-organisms on habitat invasibility. Recent studies have shown that both natural succession and successful invasion by exotic plants is at least partly driven by the positive or negative plant-soil-plant feedbacks. Native plants tend to accumulate deleterious soil micro- or macro-organisms (van der Putten *et al.* 1993, Packer and Clay 2000, Klironomos 2002) and thereby experience a drop in their competitive ability. Habitats with soils having the capacity to build up such negative feedback may be distinguished by a high invasion resistance.

There is evidence that some types of habitats tend to be particularly sensitive to plant invasions, such as riparian habitats (Lonsdale 1999). In contrast, dense or mature forests, arid habitats, salt marshes and high mountain habitats tend to have relatively few non-natives. However, habitat should not be regarded as a trait that influences invasibility by itself; rather, differences in invasibility among types of habitats appear to be based on the specific combination of factors discussed above, and listed in Appendix 1, that either increase of decrease the risk of invasibility.

Only a few studies address habitat invasibility by higher trophic levels so that Hairston *et al.*'s (1960) hypothesis discussed above cannot be reliably tested. Review of biocontrol projects provide at least some evidence that local invasion by herbivores may considerably depend on the resident pool of natural enemies. However, data from biocontrol projects are of little use to assess the relative role of resource availability and natural enemies in the establishment of exotic species, because resources (weeds or insect pests) are superabundant when the biological control agent is first introduced.

2 Establishment

Establishment, or naturalization, is usually defined as the apparent persistence of a population. The vast majority of populations of non-indigenous populations do not become established. There are numerous challenges in getting successfully established, including i) the risk of extinction due to random events, hostile climate, or genetic bottlenecks, ii) inadequacies in nutrients, hosts or mates, or iii) competitors or natural enemies.

How does a species or genotype become successfully established in a new geographic range? Studies dealing with that question have focused on identifying environmental forces that impede establishment, particular circumstances of an introduction and specific species' traits that might enable a species to overcome that impediment.

In this chapter, we will review and discuss aspects of the release events, of the environmental context and of species traits separately. However, as noted above, many of these aspects are strongly interrelated, and are therefore best explained by considering all aspects at the same time.

2.1 Characteristics of release events and rate of establishment

A common feature of almost all invasion events is that the initial population size of the introduced species or genotype is small. As will be discussed below, there are numerous threats to small populations, including stochastic processes. It is therefore no surprise that a large number of retrospective and experimental studies provide evidence that the probability of a species becoming established invariably increased with the magnitude of introduction effort (Appendix 2). This holds both for the number of individuals released and the number of introduction attempts.

In an experimental study, Grevstad (1999) tested how the initial size of a release affects the probability of successful establishment of two classical biological control agents, the chrysomelids *Galerucella calmariensis* and *G. pusilla*, that have been introduced to North America against the exotic weed purple loosestrife (*Lythrum salicaria*). For both beetles, the probability of population establishment as well as population growth rate increased with release size. These results are in agreement with other studies with biological control agents (Memmott *et al.* 1998). However, even very small initial population densities can establish and persist, for example, one female out of 20 individual releases of *G. calmariensis* founded a population that persisted for at least three years (Grevstad 1999).

No pattern between time since introduction and successful establishment has been observed for birds. In a recent assessment of weed invasion in Florida, Pemberton (2000) showed that the number of years a plant species has been sold by one of the most important plant nursery in Florida significantly positively correlated with the risk of establishment in the wild. This pattern may be explained either by time since first introduction, or by the number of releases. In any case, this study and all other studies cited above provide evidence that the more propagules of an exotic species are introduced into a new region, the higher the risk of establishment.

This clearly suggests that demographic factors play a central role in the early establishment of invading species. For example, small populations are threatened by stochastic extinction. Forces of stochasticity that can affect population persistence can be grouped into three categories: demographic, environmental and genetic. Demographic stochasticity refers to the chance variation in survival and reproductive rates in very small populations. Environmental stochasticity usually reflects the impact of random variation in the environment as it influences a population. Floods, fires and other catastrophes can be considered as extreme forms of environmental stochasticity. Finally, forces affecting genetic stochasticity involve founder events, genetic bottlenecks, and genetic drift. Bottlenecks and low effective population sizes reduce genetic variation, but directional selection during the early stages of population establishment can also reduce genetic variation (NAS 2002).

An additional effect which may drive populations to extinction is the Allee effect. An Allee effect occurs when low-density populations reach a point at which reducing density further decreases survival or reproduction, e.g. due to difficulties in locating mates (positive density-dependence). Species that are subject to an Allee effect may also be more vulnerable to extinction due to stochastic processes because the population size below which they cannot recover from an unfavourable event will be larger than for other species.

In summary, any kind of increase in the number of propagules, be it by the number of individuals released per introduction, or by the number of separate introduction events, will reduce the risk of extinction of small populations by stochastic processes. A relatively large number of individuals per introduction will reduce the risk of Allee effects or genetic inbreeding, while several small releases increase the chances that at least a few of the small populations will survive in spite of demographic or environmental stochastic processes.

2.2 The environmental context

Abiotic and biotic factors will also determine whether a new range is habitable by an immigrant. Abiotic factors that may promote establishment include a climatic match between donor and new area as well as disturbance. Biotic factors may include availability of hosts, competitors, antagonists and mutualists. Disturbance, resource availability and biotic factors have already been discussed as characteristics of the potentially invaded habitat in chapter 2.

The likelihood of establishment will be affected by the ability of the immigrant species to tolerate the climatic conditions it encounters in the new habitat. Computer-based climate-matching programmes have been developed to predict the chances of establishment as well as the potential geographic range that can be colonized by the immigrant. 'Climex' is among the most widely used programmes.

There is ample evidence that a large number of immigrant founder populations are unable to tolerate climatic conditions in the new range, and will therefore become extinct (Crawley 1986). Similarly, establishment of herbivorous insects with winter dormancy is unlikely if an insect moved between the Northern Hemisphere and the Southern Hemisphere, due to asynchronisation of the insect's life-cycle with the climate and host-plant availability. Also, stochastic variation in the physical environment can affect immigrant populations, even when average climatic conditions at a site favour establishment and growth in most years.

However, it remains a matter of debate how effectively climate-matching models can predict the likelihood of establishment or invasion in less obvious cases, e.g. when key parameters such as cold-hardiness are unknown, or even known to match between the donor and the new range. Usually, each species has a specific set of requirements for climatic conditions that has to be fulfilled in order to make a new range invasible. For example, for univoltine moths with root-feeding larvae, temperature in late fall may be the key to whether or not the species is able to complete its life-cycle in a new environment. Unfortunately, the critical requirements of an immigrant species in terms of the mean and variation in temperature, rainfall or other factors are often unknown, and it can only be hoped that relevant or correlated parameters have been included in the model. Furthermore, since genetic or phenotypic variation and plasticity of a specific trait will normally be unknown, it will always be difficult to make reliable predictions as to the fate of the immigrant population.

2.3 Species traits

As discussed above, there are numerous factors that can influence the likelihood of establishment of an immigrant population. These factors can be classified in stochastic and in abiotic and biotic environmental forces. Obviously, these processes may affect different species or genotypes differently, and it is this variation that has attracted the interest of ecologists over decades (Elton 1958). Below, species traits of organisms which have been shown to affect, or which are believed to affect, the likelihood of successful establishment in a new area are discussed.

2.3.1 Reproductive system

In general, any life-history trait that reduces the risk of extinction due to stochastic processes should increase the likelihood of successful establishment. For example, there appears to be a close relation between reproductive system and the population's ability to become established. Theory predicts that the population size required for persistence of clonal or parthenogenic species is smaller than for those for species that reproduce sexually. One reason for this is that small outcrossing populations are prone to outbreeding depression. Indeed, a few multi-species and several monographic studies provide evidence that there is an association between the ability to reproduce asexually (vegetative reproduction, apomixis) and successful establishment in a new range for various organisms (Appendix 3, for references see Niemelä and Mattson 1996). Clonal propagation is especially prevalent among invasive aquatic weeds (Barrett *et al.* 1993). Also, species with the capacity for autonomous self-pollination, so called 'selfing', are also favoured among immigrants (Pannel and Barrett 1998).

2.3.2 Population growth rate

Menges (1990, 1991, 1992) explored the inter-relationship of environmental stochasticity and demographic processes such as intrinsic rate of increase on the one hand, and persistence of plant populations on the other. He demonstrated that the higher the growth rate of a population, the lower the risk of extinction due to environmental stochasticity. Comparative studies with invading and non-invading species are in agreement with these conclusions: life-history traits related to population growth rate, such as number of offspring or broods per season, have been found to be positively correlated with the likelihood of establishment (Appendix 3). However, results of such multi-species comparisons should be treated with caution. Most studies documenting such a relationship have been done on deliberately introduced birds, and there appears to be the possibility of a confounding effect between parameters that facilitate the rearing in confinement, and the number of birds released into the new environment (Duncan 1997).

2.3.3 Dormancy

Another life-history trait that can buffer against environmental stochasticity is seed dormancy and germination cuing; indeed, Cousens and Mortimer (1995) found that both dormancy and germination cuing are widespread in many agricultural (and predominantly non-indigenous) weeds in North America.

2.3.4 Size of native range, history of range expansion

Although not a life-history trait in itself, a broad native range may be an indicator for a species' ability to survive under various climatic conditions. Consequently, the size of the native range of invading species is positively correlated with the likelihood of establishment (Appendix 3). Similarly, the history of successful invasion elsewhere may also be considered, among others, as an indicator that a species is pre-adapted or can adapt to new climatic conditions. However, how often invaders colonize areas which have a climate that is comparable to the ones in the native range, and how often and which invaders indeed were able to adapt to different abiotic environments, remains to be tested.

2.3.5 Phenotypic plasticity

Many species traits have evolved, within their phylogenetic constraints, as a response to the biotic forces acting on a species in the different habitats of its native range. Some of species traits are expressed in a largely invariate form, other may vary considerably under different environmental conditions. Even though rarely tested in multi-species comparisons, phenotypic plasticity is considered as a key characteristic common to many invasive species. In a recent review, Daehler (2003) found that exotic plants consistently show a higher phenotypic plasticity than co-occurring related plants. Most observations of greater phenotypic plasticity in invaders involved changes in biomass allocation patterns in response to different environmental conditions, which allows invaders to succeed in a wider range of environments and respond more quickly to changes in resource availability.

2.4 Establishment of GMOs outside the crop field

A few studies have experimentally tested whether genetic modification of crop plants can increase the likelihood of successful establishment outside the cultivated fields. Linder and Schmitt (1995) assessed the risk that seed-oil-modification transgenes will increase the persistence of feral *Brassica napus* canola and interspecific hybrids of *B. napus* canola and the wild *Brassica rapa*, a weedy relative. In two different regions, Linder and Schmitt (1995) tested whether buried seeds of transgenic high-stearate canola had increased survivorship and dormancy, compared to nontransgenic null segregant and parental lines. In one region, no differences could be found between high-stearate canola and its controls. However, in the other region, seeds of the transgenic line exhibited no detectable exit from the seed bank, whereas both controls had significant rates of exit. This suggests that escaped seeds from the transgenic high-stearate canola may persist under certain environmental conditions for a longer period than its parental line.

In a second experiment, Linder and Schmitt (1995) measured the relative ability of two different transgenic lines of canola and the respective controls to emerge from different depths in the soil and their subsequent seedling vigour. While the transgenic high-stearate canola emerged more slowly and had significantly less biomass than its parental line, no difference could be found between the high-laurate canola and its parental lines. The different results for the two oil-modification transgenes suggest that even transgenes with similar functions should be considered on a case-by-case basis.

A seminal study on the risk of increased persistence of GMOs inside and outside crop fields was carried out by Mick Crawley and his colleagues. This study will be discussed in chapter 6.

2.5 Summary

Various species traits affect the critical density threshold below which a population is threatened by extinction. Species traits such as reproductive system, dispersal mechanism, number of offspring, or length of juvenile period can affect this density threshold, and it therefore comes as no surprise that in multi-species comparisons these traits often correlated with increased likelihood of successful establishment. On the other hand, species traits that reduce the effective population size (the actual number of reproducing genotypes), such as sexual reproduction or highly evolved pollination systems are negatively correlated with the likelihood of successful establishment. These demographic patterns are widespread in nature and clearly not restricted to invasive species.

In addition, the size of the native range and the geographic origin are good predictors for the likelihood of successful establishment of an introduced species. These attributes are not species-traits by themselves, but rather indicators for a combination of species traits that often harbour considerable phenotypic plasticity.

3 Population build-up and spread

Only some non-indigenous species that become established in a new region will rapidly increase in population size and simultaneously spread. In this demographic and geographic transition, which is often called a biotic invasion in the narrow sense, the species is no longer at risk of becoming extinct through stochastic forces. This chapter addresses the question of why some species make the transition from low rates of population growth to high rates, i.e., shift from surviving to being invasive.

An immigrant, established population will become a successful invader only if the population is able to increase in abundance and spread from its point of entry. Examination of the dynamics of range expansion for invasive plant species (for which information exists) indicates a characteristic pattern of population spread: once established in a new range, populations tend to remain small and localized, often for long periods, before a sudden explosive increase in local density and range expansion occurs (e.g., Lonsdale 1993, Weber and Schmid 1998). The initial phase has been termed the lag phase and can last for several decades in plant invasions. In comparison, few quantitative studies have been conducted of range expansion and invasion for exotic animals. The current evidence suggests that animal invasions do not show an extended lag phase. It is likely that this difference reflects differences in the level of interspecific competition among different trophic levels. As discussed in chapter 2, non-indigenous plants may have to compete primarily with the native plant species for available resources. Interspecific competition among newly established and resident insects is often low so that invading insects may be able to increase their population size quickly in areas where pressure from native generalist predators or parasitoids is low (National Academy of Sciences 2002).

3.1 Predictors for increased risk of biotic invasion

3.1.1 History of invasion

Probably the single best general predictor of a high risk of biotic invasions is that the species is known to have been invasive elsewhere in its exotic range (Appendix 3). This criteria has been found useful for plants in Australia (Scott and Panetta 1993), Hawaiian passerines (Moulton and Pimm 1983), vertebrates (Ehrlich 1989) and insects (Crawley 1987). For example, in Hawaii 76% of the invasive plants species invade elsewhere and only 28% of the non-invasive group do (Reichard 2001).

3.1.2 Taxonomy

Interestingly, not only does the invasion history of the species under investigation provide useful predictions, but also if other species within the same genus or family are invasive, this may correlate with the invasive ability of the target species (Appendix 3). However, using taxonomic relationships to evaluate the risk of invasiveness does not seem advisable, since within a family or genus there may be very aggressive weeds and rare, non-competitive species (Reichard 2001).

3.1.3 Population growth

Numerous species traits that increase the likelihood of successful establishment also correlate with increased risk of biotic invasion. In particular, species traits that affect population growth rate, such as a large number of offspring, small offspring size, short juvenile period, a long flowering period and simple dispersal mechanisms have been identified to facilitate biotic invasion (Appendix 3).

Vegetative reproduction has also been shown to be positively associated with an increased risk of invasion in plants.

3.1.4 Resistance against natural enemies

Habitats which experience shifts in trophic interactions may become vulnerable to invasion by species that have evolved in their native range under comparable conditions. For example, in the prairies of the north-western states of America plant species evolved under moderate and sporadic grazing pressure of migrating bison. Since more than 50 years, large parts of the prairies have been heavily grazed by introduced cattle, which most probably has facilitated the invasion of exotic plant species that evolved under high grazing pressure in their native range and are physically or chemically defended against cattle grazing (Mack and Thompson 1982).

3.1.5 Ability to alter the environment

Another characteristic of various invading plant species is their ability to alter the environment. The introduction of salt on the soil surface in the case of *Tamarix* or root-modulating plants can alter species composition and vegetation succession. In addition, various knapweeds of the general *Centaurea* and *Acroptilon* leak chemicals from the roots which have significant negative impact on neighbouring plants in the exotic range (Ridenour and Callaway 2001, Bais *et al*. 2003, Stermitz *et al*. 2003), while old neighbours from the native range do not seem to suffer from these exudates (Callaway and Aschehoug 2000). Simulation models indicate that in North America the exotic weed *Acroptilon repens* can invade native grassland communities only if native species are sensitive to allelopathy from the invader (Goslee *et al.* 2001).

3.1.6 Potential for evolutionary change

The evolutionary genetics of invasive species has been relatively unexplored, but recent studies suggest that the invasion success might depend more heavily on ability to respond to natural selection than on tolerance or plasticity. One explanation for the lag phase in the invasion process of plants which has been put forward is that populations may be poorly adapted initially, but after a period of selection they may be able to increase population growth rate and start expanding (Müller-Schärer and Steinger 2003). Hence, invasion success could be facilitated by the presence of genetic substrate in source populations upon which natural selection could act. Genetic attributes such as additive genetic variance, epistasis, genetic trade-offs and possibly genomic rearrangements are believed to facilitate invasion success (Lee 2002).

A source of variation that can favour the evolutionary diversification of invading species is the mixing of genes through hybridisation between different populations that are allopatric in their native range but occur together when introduced into the same new region. Hybridisation with native species or subspecies will also lead to increased variation (Lee 2002).

3.2 Biotic invasions in Europe

There is currently limited information available on which species traits are correlated with increased risk of population build-up and spread in Europe. The only multi-species study we are aware of comparing 'successful' and 'unsuccessful' alien plant species in Europe was carried out by Pysek *et al.* (1995) for the territory of the Czech Republic. In this work, an exotic species was considered 'unsuccessful' when it either was absent or rare in specific habitats, while a species was considered 'successful' when it had a scattered distribution over the the whole territory, was locally abundant, or was common and abundant within the whole territory. This classification does not allow to distinguish between the two steps 'successful establishment' (chapter 3) and successful population build-up and spread (this chapter), so the results should be discussed with regard to successful completion of both invasion steps. Of the species traits tested by Pysek *et al.* (1995), only life form (e.g. therophytes, hemicrytophytes) was correlated with invasion success, while neither origin of species, nor life strategy (e.g. ruderal species), dispersal agent, nor mode of spread differed significantly between 'unsuccessful' and 'successful' exotic plant species. Further studies are needed to elucidate those species traits that correlate with an increased risk of invasiveness in European habitats.

Even though it has not been rigorously tested, there is little doubt that history of invasion is also a good predictor for the increased likelihood of invasiveness of exotic species for Europe (Williamson 1999).

3.3 The risk of biotic invasion by GMOs

Hybridisation between transgenic crops and related species can introduce novel traits into the wild species, but the ecological consequence of such a process is often unknown. Snow *et al.* (2003) report the first empirical evidence that wild plants can benefit from transgenes under natural conditions. Cultivated sunflower is known to hybridise frequently with wild sunflowers in North America. Back-crossed wild sunflower populations containing a crop-developed Bt transgene, Cry1Ac, had strongly reduced feeding damage by Lepidoptera, while damage by several weevil and fly species was unaffected. The results suggest that reduced herbivory caused transgenic plants to produce an average of 55% more seeds relative to nontransgenic controls. Snow *et al.* (2003) expect that, if Bt sunflowers are released commercially, the Bt genes will spread to wild and weedy populations, limit damage from susceptible herbivores on these plants, and increase seed production when these herbivores are common.

One approach which has often been recommended when assessing the risk associated with transgenic plants is to test the relative fitness of wild susceptible and transgenic isolines in the absence of the factor to which the transgenic has been made resistant to. For example, a herbicide-resistant transgenic plant should be grown together with its wild isoline under herbicide-free conditions to assess the costs of herbicide resistance. The notion is then that if a particular genotype produces fewer seeds or has a reduced survival ability compared to wild-type plants, it will be less likely to invade natural communities. The assumption underlying these predictions is that changes in performance of individuals will be reflected in changes in the invasiveness of the species. Bergelson (1994) demonstrated that this is not necessarily true in every case. In a pair of experiments, he measured how a gene conferring resistance to the family of sulfonylura herbicides influences the performance and the invasiveness of the weedy annual *Arabidopsis thaliana* when herbicides are absent. The first experiment was designed to test the relative fitness of resistant and susceptible isolines under field conditions. Bergelson found that susceptible individuals outperformed resistant genotypes, but that the differences were only significant at high levels of background competition. To assess whether this short-term cost is translated into reduced invasiveness, Bergelson carried out a second experiment in which he simulated an invasion by introducing either resistant or susceptible plants into replicated plots of background vegetation and measured the number of *Arabidopsis* plants established in the following generation. He found no evidence that the reproductive disadvantage of resistant genotypes translated into reduced invasiveness. Bergelson hypothesized that the absence of a detectable difference in invasiveness can be traced to the fact that space rather than seed production limited recruitment in his experiment.

This example illustrates that a risk assessment should not only try to quantify changes in species traits, but should also assess the effect of such changes on the population dynamics of the transgenic organism. Various models (see chapter 6) have been developed that allow a quantitative assessment of the effect of a change in a species trait on the finite rate of population growth.

4 Predictive systems

In the previous chapters, a review was made of factors that explain, to some extent, why some organisms are able to persist and spread, outcompete natives, and alter ecosystems. All these traits have been identified in retrospective studies. Retrospective studies try to identify why an event has occurred using statistical analysis of experimental observations.

From an administrative point of view, the ability to identify potentially invasive exotic or transgenic species or genotypes could have enormous benefits. Prediction systems are particularly useful when a decision has to be made about the deliberate introduction of an exotic and/or genetically modified organisms, or when priorities need to be set with regard to the control of already established non-indigenous species.

However, prediction is not explanation. Prediction is the generation of statements about the likelihood that events will occur (Williamson 1996). In this chapter, published and unpublished systems of prediction, usually termed ecological risk assessments, will be presented and assessed with regard to the certainty and confidence in predicting invasion events.

Hitherto, the prediction of biotic invasions has been based largely on extrapolation for species that already have a record of invasiveness. The ‘World’s Worst Weeds’ (Holm *et al.* 1991) is testimony to the recurrence of some species as invaders in many ranges. The scientific panel of the National Academy of Sciences, USA, concluded in their report on ’Predicting Invasions of Non-indigenous Plants and Plant Pests’ (2002) that ‘the record of a plant’s invasiveness in other geographic areas beyond its native range remains the most reliable predictor of its ability to establish and invade’. However, the panel also argues that expert judgement of a species’ potential impact in new ranges has limitations, such as its subjective nature. Of course, this approach is not applicable for the many species that have no history of spread beyond their native range.

This chapter examines more elaborate systems for predicting the invasiveness of organisms. The systems have been developed for and applied to plants and plant pests, and they therefore will be presented in this context.

4.1 Biotic and abiotic attributes used in predictive systems

Various species traits that have been identified as correlating with increased or reduced risk of invasiveness (Appendix 3) have been used in studies that tried to predict the risk of invasiveness for groups of organisms in a designed area. Since it is often impossible to collect detailed biological information, emphasis has been put on collecting biological information from published floras or faunas. The number of biological characters known for large samples of species is usually limited. For example, traits such as life-form, stem height or flowering period may be easily available for plants, and number of offspring, number of broods or migration/no migration for birds. For data sets that are restricted to a relatively small number of organisms, such as pines, further data may be collected from all species included in the study. These studies usually provide the best insight as to potential mechanisms that may underlie the risk of increased invasiveness (Grotkopp *et al.* 2002). An alternative approach is to make qualitative statements about species traits for which no quantitative data are available.

The establishment of non-indigenous pathogens or animals is subject to the temporal or spatial availability of a suitable host. This is particularly relevant for species with a restricted host-range, e.g. herbivores feeding on only one host plant genus. However, detailed information on the fundamental host-range (the range of hosts on which a species can complete its life-cycle) is often not known in detail, and to simply assume the potential host-range in the new area from what hosts are used in the native range is not appropriate (Schaffner 2001).

Besides biotic attributes, a number of abiotic (mainly biogeographic) attributes as well as information on the history of the species are included in predictive systems. For example, the invasion history of a species, which has been shown to be one of the best predictors for risk of increased invasiveness in a new range, is almost always included in risk assessment schemes (see below). Other attributes that are considered are climate matching and the geographic distribution. The likelihood of establishment is affected by the general climatic match between the donor habitat (which may be an area outside the native range and where the species has already become invasive) and the new habitat of the immigrant species.

4.2 Pest risk assessment systems

Risk is the product of the likelihood of an event or process and its consequences. Although predicting the likelihood of invasion by non-indigenous species has much appeal and is a major ecological challenge, it is risk that must be evaluated. Also, if only the likelihood of a non-indigenous species' becoming established in a new environment is considered, it is difficult to apply the level of uncertainty in this prediction fully in decision-making. But, as outlined in the NAS report (2002), if the consequences of an invasion are considered, uncertainty can be incorporated into the evaluation of risk.

To illustrate risk assessment protocols currently in use, two systems will be presented in detail. The first system is currently applied by USDA with imported solid-wood packing materials. The protocol consists of two parts, A) a qualitative assessment of likelihood of pest introduction and B) consequences of introduction. The likelihood of introduction is determined by a series of independent events that must all occur for the immigrant species to develop an invasive population. Therefore, the final score of the likelihood of introduction is the multiplication of probabilities of these events. Consequences of introduction are essentially the sum of individual consequences which may carry different weights. The final pest risk potential is based on joint consideration of likelihood of introduction and consequences of introduction (Fig. 2).

Figure 2. Qualitative Pest Risk Assessment procedure proposed for use with imported solid-wood packing materials (US Department of Agriculture 2000).

A) Pest Risk Potential

Likelihood of Introduction	Consequences of Introduction		
	High (H)	Moderate (M)	Low (L)
High (H)	High	High	Moderate
Moderate (M)	High	Moderate	Moderate
Low (L)	Moderate or Low	Moderate or Low	Low

B) Likelihood of Introduction

Likelihood of association with commodity at point of origin		**Entry potential**	
- Repeated historical interception	→ H *or*	- Repeated historical interception	→ H *or*
- Capacity for large population increase - Wide distribution through range of host(s) - Multiple generations or extended period for colonizing hosts - Extended survival on or in plant host - Not likely to be separated from host	≥ 2 = H → 1 = M 0 = L	- One or more stages likely to survive transport - Not likely to be separated from host - Difficult to detect	≥ 2 = H → 1 = M 0 = L

Establishment potential		**Spread potential**	
- historical record of establishment	→ H *or*	- Capable of dispersing > several km per year - Demonstrated redistribution via human-assisted transport - High reproductive potential - showed ability to use new hosts - Hosts contiguously distributed - New populations difficult to detect - Low likelihood of eradication of new populations - Broad host range - Potential to be more efficient vector	≥ 5 = H →2-4 = M ≤ 1 = L
- There is climate matching - Suitable climate and hosts near point of entry - Documented ability to use new hosts - Active host search or vectored - High propagule pressure	≥ 2 = H → 1 = M 0 = L		

Likelihood of Introduction = Minimal

Likelihood of association:	Entry potential:	Establishment potential:	Spread potential:
- High - Moderate - Low	- High - Moderate - Low	- High - Moderate - Low	- High - Moderate - Low

C) Consequences of Introduction

Economic damage potential		**Environmental damage potential**	
- attacks hosts with significant commercial value - causes or predisposes hosts to mortality - causes decreased value of hosts - may cause loss of markets (quarantine) - demonstrated ability to develop more virulent strains or biotypes - no known control measures	≥ 4 = H →2-3 = M ≤ 1 = L	- expected to cause significant direct environmental effects	→ H
		- expected to directly impact endangered or threatened species	→ H *or*
		- expected to indirectly impact endangered or threatened species - may attack host with limited range - introduction likely to initiate control measures with adverse environmental effects - showed ability to develop more virulent strains or biotypes	≥ 2 = H → 1 = M 0 = L

Social and political considerations	
- damage caused by organisms will engender public concern - introduction of organism will likely cause domestic political repression - introduction of organism will likely have international tgrade repercussions - known control measures likely to have limited acceptance	≥ 2 = H → 1 = M 0 = L

Rating for

CONSEQUENCES OF INTRODUCTION:

Is determined as

- Maximum of economic and environmental damage potentials, provided both are not low.
- Otherwise, rating is moderate when social and political considerations are high or moderate and low when these considerations are low.

The second system presented here has been elaborated to determine the weed potential of new plant introductions to Australia (Pheloung 1995). Plant species that are not included on either prohibited or permitted lists of species are to be assessed before entry by a formal Weed Risk Assessment (WRA) system. In this system, answers are sought for questions on historical, bio-geographical and biological/ecological details of the candidate (Table 1; Pheloung 1955). The score generated by the procedure determines which of three recommendations, reject, evaluate or accept, will result.

In contrast to most other risk assessment systems, including the USDA system presented above, the WRA system has been tested by analysis of its performance for 370 plant species, representing weedy and non-weedy species. In the optimized WRA system, all serious weeds, and most minor weeds, were rejected or required evaluation while only 7% of non-weeds were rejected.

Weber and Gut (unpublished) designed a risk assessment protocol for potentially invasive plant species in central Europe. They adapted existing protocols to the specific demands of European countries. A pre-evaluation step excludes species that are officially controlled, widespread, or intended to use in protected cultures only. Species eligible for risk assessment are then classified into three categories (high risk, further observation, low risk), by rating them according to various bio-geographical (e.g., climate match, range size, history as a weed elsewhere) and ecological aspects (e.g., vegetative growth, dispersal mode, life-form).

Table 1. Questionnaire of the Australian Weed Risk Assessment System (Pheloung 1995).

Answer *yes* or *no* , or leave blank, unless otherwise indicated

Botanical name:　　　Outcome:
Common Name:　　　Score:
Assessor:

			Biogeography/ historical	
A	**1**	*Domestication/ Cultivation*	1.01 Is the species highly domesticated?	
C			1.02 Has the species become naturalised where grown?	
C			1.03 Does the species have weedy races?	
	2	*Climate and Distribution*	2.01 Species suited to Australian climates (0-low; 1-intermediate; 2-high)	
			2.02 Quality of climate match data (0-low; 1-intermediate; 2-high)	
C			2.03 Broad climate suitability (environmental versatility)	
C			2.04 Native or naturalised in regions with extended dry periods	
			2.05 Does the species have a history of repeated introductions outside its natural range?	
C	**3**	*Weed Elsewhere*	3.01 Naturalised beyond native range	
N			3.02 Garden/amenity/disturbance weed	
A			3.03 Weed of agriculture	
E			3.04 Environmental weed	
			3.05 Congeneric weed	
			Biology/Ecology	
A	**4**	*Undesirable Traits*	4.01 Produces spines, thorns or burrs	
C			4.02 Allelopathic	
C			4.03 Parasitic	
A			4.04 Unpalatable to grazing animals	
C			4.05 Toxic to animals	
C			4.06 Host for recognised pests and pathogens	
N			4.07 Causes allergies or is otherwise toxic to humans	
E			4.08 Creates a fire hazard in natural ecosystems	
E			4.09 Is a shade tolerant plant at some stage of its life cycle	
E			4.10 Grows on infertile soils	
E			4.11 Climbing or smothering growth habit	
E			4.12 Forms dense thickets	
E	**5**	*Plant type*	5.01 Aquatic	
C			5.02 Grass	
E			5.03 Nitrogen fixing woody plant	
C			5.04 Geophyte	
C	**6**	*Reproduction*	6.01 Evidence of substantial reproductive failure in native habitat	
C			6.02 Produces viable seed.	
C			6.03 Hybridises naturally	
C			6.04 Self-compatible or apomictic	
C			6.05 Requires specialist pollinators	
C			6.06 Reproduction by vegetative fragmentation	
C			6.07 Minimum generative time (years)	
A	**7**	*Dispersal mechanisms*	7.01 Propagules likely to be dispersed unintentionally (plants growing in heavily trafficked areas)	
C			7.02 Propagules dispersed intentionally by people	
A			7.03 Propagules likely to disperse as a produce contaminant	
C			7.04 Propagules adapted to wind dispersal	
E			7.05 Propagules buoyant	
E			7.06 Propagules bird dispersed	
C			7.07 Propagules dispersed by other animals (externally)	
C			7.08 Propagules survive passage through the gut	
C	**8**	*Persistance attributes*	8.01 Prolific seed production (>2000/m2)	
A			8.02 Evidence that a persistent propagule bank is formed (>1 yr)	
A			8.03 Well controlled by herbicides	
A			8.04 Tolerates, or benefits from, mutilation or cultivation	
E			8.05 Effective natural enemies present in Australia	

A= agricultural, E = environmental, N = nuisance, C=combined

It has been stressed that the process of conducting a qualitative risk assessment is at least as valuable as the specific risk values that are produced, because the process, when carefully documented, provides a mechanism for assembling and synthesizing relevant information and knowledge (National Academy of Sciences 2002).

4.3 Accuracy

The accuracy of a screening method in identifying invaders can only be measured after the introduction of the species, once it is known which have succeeded and which have failed as invaders. Accuracy is defined as

$$A_i = (I_r/I_t) \text{ x } 100$$

where I_r is the number of invaders that were rejected by the system, and I_t is the total number of invaders assessed. Similarly, its accuracy at identifying non-invaders is calculated as

$$A_n = (N_a/N_{t)} \text{ x } 100$$

, where N_a is the number of non-invaders accepted and N_t the total number of non-invaders assessed (Smith *et al*., 1999).

Accuracy rates of retrospective studies can be fairly high (Appendix 4). For plants, the traits included in the final model (Appendix 4) explained on average 58% (range 40-88%) of the variance or deviance. Furthermore, even though the discriminant analysis carried out by Rejmanek and Richardson (1996) to distinguish invasive from non-invasive pines explained ‘only’ 78% of the variance, it nevertheless classified all pine species correctly. Comparable accuracy rates were obtained in retrospective studies with birds (Appendix 4).

The taxonomic coverage of animal invasion studies is highly biased. So far, multi-species comparisons have been published for birds only. Studies on insects and fish would be particularly valuable because they are frequently introduced both intentionally and unintentionally, and often cause substantial ecological change and economic damages. Kolar and Lodge (2001) reported that a first study on fish is in progress.

Encouraged by fairly high accuracy rates found in retrospective identifications of known weed species based solely or largely on plant characters, some go further and claim to have developed successful weed prediction systems. Indeed, the predictive power of the schemes listed in Appendix 4 ranges from moderate to high (range of the invasive species correctly classified 60-97%). The scheme developed for Europe by Weber and Gut (unpublished) achieves a predictive accuracy rate of 65 % for invasive species. Assessments of the accuracy rate of predictive systems have so far exclusively been made using systems dealing with plant species (Appendix 4). We are not aware of a published study that tried to develop and test a predictive system for risk of invasiveness of other organisms.

The critical question then is whether accuracy rates of 65-85% are useful in taking decisions based on such a weed risk assessment system. One possible approach to explore the relevance of recommendations of a screening system for exotic introductions is by analysing the scenarios with the help of the decision theory (Smith *et al.*, 1999).

4.4 Invasion predictions and decision theory

Organisms generally become pests at low rate. The overall base-rate R that species become pests is a product of three other probabilities (Williamson and Fitter 1996): the rate at which imported species become casuals, the rate of establishment of casual species, and the rate of conversion of established species into pests. Williamson and Fitter (1996) estimated that around 10% of organisms introduced to a new environment become casuals, 10% of these become naturalized and 10% of these naturalized species go on to become pests (the “ten’s rule”). Thus, only 0.1% of the species originally introduced are expected to become pests. Rare events are difficult to forecast, since the probability of correctly predicting an event is a function of the accuracy rate and of the frequency with which that event occurs at all (the so-called ‘base-rate effect’). In this regard, it is critical to distinguish between a system’s accuracy (the proportion of events that are correctly predicted) and reliability (the rate of ‘false positives’ and ‘false negatives’ produced). False positives are predictions that an event will happen but it doesn’t, while false negatives are predictions that an event will not occur, but in fact it does. To illustrate the problem of rare events and the risk of false positives and false negatives, imagine that the ability of a weather forecaster to predict rain is 90%. However, if rain only occurs on 1% of days, the impressive accuracy rate makes many more mistakes (10% of 99% of days) than correct predictions (90% of 1% of days). In other words, at such a low base-rate effect, we would be far better off ignoring forecasts, unless we have a mortal terror of rain (Matthews 1996).

Similarly, because of the rarity of successful biological invasions compared with the number of imported species, the usefulness of weed risk assessment systems needs to be assessed in the context of the base-rate effect involved in calculating the probability of correctly predicting invasion success.

As outlined above, accuracy is the proportion of a group of known invaders or non-invaders correctly identified. Reliability, on the other hand, is the proportion of wrong decisions. In the context of this review, we will focus on two aspects of reliability: the probability that a species accepted will become an invader (P_{ai}), where

$P_{ai} = I_a/(N_a + I_a)$,

And the probability that a rejected species would have been an invader (P_{ri}), where

$P_{ri} = I_r/(N_r + I_r)$.

Reliability, which is the ultimate test of the usefulness of invasion risk assessment systems, depends on the interaction of accuracy and base-rate. Matthews (1996, 1997) described a method to construct contingency tables to explore the interaction between base-rate and accuracy. Using this approach, Smith *et al.* (1999) calculated a number of scenarios with varying accuracies and base rates (see Table 2).

The key conclusions from the scenarios calculated by Smith *et al.*(1999) is that a screen using an accuracy rate of 85% can, even at a relatively broad range of base-rates, significantly reduce the chance that an exotic plant is considered harmless while it is in fact an invasive weed. The caveat is, though, that base rates of 2% and less will lead to a lot of 'false positives'. For example, using a base-rate of 2% and a high accuracy of 85%, roughly nine out of ten plants identified as potential weeds are not likely to become weeds.

Table 2. The effect of accuracy of a screening method for invasive plant species, and the base-rate at which imported species become weeds (after Smith *et al.* 1999).

	Number of weed species	Number of non-weed species	Totals
A: Accuracy = 85%, base rate = 2%			
Forecast of weed	17	147	164
Forecast of non-weed	3	833	836
Totals	20	980	1000
Proportion of weed forecasts correct (P_{ri})			10%
Proportion of non-weed forecasts incorrect (P_{ai})			0.36%
B: Accuracy = 85%, base rate = 17%			
Forecast of weed	144.5	124.5	269
Forecast of non-weed	25.5	705.5	731
Totals	170	830	1000
Proportion of weed forecasts correct (P_{ri})			54%
Proportion of non-weed forecasts incorrect (P_{ai})			3.5%
C: Accuracy = 65%, base rate = 2%			
Forecast of weed	13	343	356
Forecast of non-weed	7	637	644
Totals	20	980	1000
Proportion of weed forecasts correct (P_{ri})	3.7%		
Proportion of non-weed forecasts incorrect (P_{ai})		1.1%	

Based on these calculations, Smith *et al.* (1999) suggested that a national early warning system for invaders should not focus on picking the potential pests from amongst imported species, but rather from amongst naturalized species. This is because the base-rate for the transition from naturalized to pest status R_w is by definition much higher than R (see above). One should, however, keep in mind that there is of course a trade-off between difficulty of controlling a species once it is naturalized and the unreliability of screens at earlier steps of the invasion process.

4.5 Development of risk assessments in Europe

The European and Mediterranean Plant Protection Organisation (EPPO, in prep) has designed a pest risk assessment scheme that aims to assess the risks posed by unintentional introductions of invertebrate and pathogen pests to cultivated plants. The scheme consists of two major steps: first, a series of questions are listed that should help to screen out species that clearly pose no risk to a clearly defined area. In a second step, a number of questions need to be answered to assess the probability that a pest can enter, establish and cause significant economic, environmental and social impacts in the area under consideration. Recently, the EPPO pest risk assessment scheme has also been adopted to assess the risks posed by pest plants, including exotic plant species (Buholzer, personal communication), and for freshwater fish pest risk assessment (CEFAS, Copp *et al.* 2003).

Even though the EPPO pest risk assessment schemes is considered a useful basis on which to assess the risk posed by selected exotic species, these schemes have not been validated so far. To our knowledge, the scheme developed for exotic plant species by Weber and Gut (unpublished) is the only validated risk assessment scheme for exotic species in Europe so far (though with moderate power; see Appendix 4).

In 2003, an EU project called ‘Alarm’ has been launched that aims to fill the gap of knowledge with regard to risk assessment methods in Europe by developing novel insight into biological invasions. A project team consisting of 53 partners from 26 countries set out to assess both the risk and the hazards of invasive species. The project will analyse species invasiveness and the invasibility of ecosystems for major European regions. Risk assessment methods will be established for a number of different organismal groups, including arthropods, mammals, and plant species. Validation of the analyses will involve comparison of predictions with trends in species invasiveness on other comparable biomes, such as North America.

4.6 Applicability of risk assessment systems to GMOs

Risk assessments are inherently imprecise, but they nevertheless are among the best methods to assess the potential risk of invasiveness for a more or less large number of related species. As outlined above, if there are large potential economic benefits in releasing a non-indigenous species into a new range, then economists should ignore the advice from even the best predictive systems set up to date. This is obviously also true for GMOs. Unless one can fairly accurately estimate the ecological or economic risks associated with GMOs that become invasive, the use of predictive systems as a risk assessment tool for GMOs does not seem to be appropriate. Instead, the risk of increased invasiveness of GMOs should be assessed by carrying out case studies. Risk assessment systems and the individual species and environmental traits listed in Appendix 1 and 3 should, however, be consulted in GMO risk assessment studies when designing appropriate experiments and models. In the following chapter, case studies with GMOs will be presented to demonstrate this approach.

5 Case studies

In the previous chapters, we summarized the life-history traits of various taxonomic groups that have been shown to correlate with increased invasiveness, and we asked the question whether a multi-species approach may help to reliably predict whether a newly established species may become invasive. In this chapter, we will present some case studies in which the risk of invasiveness of exotic or transgenic organisms was assessed using field experiments and/or models, for pine trees, genetically modified oilseed rape and a genetically modified fish species.

5.1 Case study 1: Ecology of transgenic oilseed rape

In 1993, Crawley *et al.* published a study in which they assessed the risk of a genetically engineered oilseed rape becoming a weed of agriculture or invasive of natural habitats. By estimating the demographic parameters of transgenic and conventional oilseed rape growing in a variety of habitats and under a range of climatic conditions, they set out to make direct comparisons of the ecological performance of three different genetic lines (control, kanamycin-tolerant transgenic and herbicide-tolerant transgenic lines). The prediction was that the tested transgenic lines would not outperform the conventional plants, since neither antibiotics nor herbicides were applied in the experiments.

Crawley *et al.* compared the demography of transgenic and conventional lines of plants in a range of habitats throughout Great Britain. The experiments were carried out over three years in 12 different habitats. To quantify the effect of the invasive potential, they estimated the finite rate of increase (λ) of different genetic lines under the variety of experimental conditions. Values of $\lambda > 1$ predict that the plant will increase in abundance under the given set of environmental conditions; values of $\lambda < 1$ predict that the plants will decline to extinction.

Oilseed rape is an annual or short-lived monocarpic perennial with a simple life cycle. In the experiment, seeds were sown in spring, flowering occurred in summer and seed was shed in autumn. The finite rate of increase can therefore be written as

$$\lambda 1 = (1\text{-d1-g}) + \text{g}(1\text{-d2})\text{F}$$

, where d1 is the proportion of seeds germinating in the first spring that die in one full year, g is the proportion of seeds germinating in the first spring, d2 is the proportion of seeds that die over winter, and F is the mean number of seeds produced per seed that germinates. Separate experiments were carried out to evaluate each component: a seed burial experiment gave estimates of d1, and a seed sowing experiment provided estimates of germination, plant survival and fecundity. Additional experimental treatments were superimposed, e.g. cultivation to reduce interspecific competition, fencing to exclude vertebrate herbivores, and chemical exclusion of molluscs).

Seedling densities, adult plant densities and mean seed production per plant varied significantly between years and between habitats within years. Also, some of the experimental treatments had major effects on plant demography. However, there was no significant overall effect of genetic line on any of the demographic parameters, nor were there any interactions between sites, years and genetic line. In two of the three years, all three genetic lines had $\lambda > 1$ on plots which were cleared of all vegetation, predicting that rape populations would increase. These λ values are based on the seeds starting life in a cultivated, competition-free environment. In contrast, the seeds produced by the first generation of our experimental plants were shed into an environment in which the competing perennial vegetation had had a full growing season to recover from cultivation. Therefore, a new estimate of λ was calculated based on the number of self-sown seedlings in year $t + 1$ to the number of seedlings arising from the experimental sowing. By calculating

$$\lambda\ 2 = \text{seedlings of generation 2/ seedlings of generation 1},$$

the invasion criterion was not realized in any of the habitats.

The authors therefore conclude that there is no evidence that oilseed rape could be invasive in undisturbed natural habitats, and no evidence that transgenic lines of rape are more invasive of, or more persistent in, disturbed habitats than their conventional counterparts. However, they stressed that, although these results suggest that herbicide-tolerant oilseed rape poses no greater threat to the environment than the conventional crop, it would be prudent to reserve judgement on the risks that might be posed by other crop species or different transgenic lines, particularly those with traits which might be expected to enhance plant performance in natural habitats.

Two reasons why this study is exemplary is that it was carried out in different habitats (in presence and absence of competitors and antagonists), and that the experiments were carried out over several experimental years. As calculated by Kareiva *et al.* (1996), any reduction of sampling effort (2 instead of 3 years, 11 instead of 12 sites etc.) would have lead to a much poorer estimate of oilseed rape rate of increase. Kareiva *et al.* (1996) therefore concluded that ‘experimental assessments of genetically modified organisms risks will require several years of data’, and also a number of different environments tested.

5.2 Case study 2: Modelling interactions between organisms, environment and disturbance

The ability to quantitatively predict invasiveness and impact of alien species are at least partly limited by the lack of suitable models that include interaction terms between species-specific traits and environmental attributes. Most invasion models use information on either the species or on environmental attributes alone to predict rates and patterns of the spread of the invasive species. The assumptions of these models used do not allow explicit investigation of the interactions between species attributes, environmental heterogeneity, and stochasticity. Because plant-environment interactions strongly influence invasion rates and patterns, this limits the predictive values of such models (Higgins and Richardson 1998).

Alternative models should integrate space, ecological processes, and stochasticity into a single predictive framework. Higgins *et al.* (1996) and Higgins and Richardson (1998) propose a spatially explicit, individual-based simulation (SEIBS) model to simulate the spread of alien pine trees from established commercial plantations into natural fynbos ecosystems in Southern Africa. The literature on pine invasions suggests that five factors (adult fecundity, dispersal ability, time to reproductive maturity, the temporal frequency of post-fire recruitment opportunities, and the survival of adults) are major determinants of spread (Richardson *et al.* 1990). The model is constructed so that each of these factors can be explicitly modelled.

The two pine types chosen for the model include most of the common invasive pines in the southern hemisphere. The R-pine (e.g. *Pinus radiata*) is typical of landscapes characterized by predictable stand-replacing fires. The second pine type, U-pine (e.g. *Pinus strobus*), occurs with unpredictable stand-replacing fires. The two pine types differ in various species traits, such as bark thickness, length of juvenile period, or shade tolerance during seedling stage. In the following, a short description of the model is given.

Model environment:

- The SEIBS model considers a two-dimensional grid of sites (100 by 200 locations). The relatively small grid was used due to computer time limitations.

- Each site is of initially equal environmental quality, but this may change during the simulation (see below).

- Time passes in discrete intervals of 1 year.

- Each simulation run was initiated with a row of mature trees along a Y-dimension edge of the grid. This row represented the edge of a commercial pine plantation. All runs were stopped when a single tree reached the Y-dimension edge opposite the site of initiation.

Disturbance and mortality:

- Two types of disturbance are considered: fire and gap creation;

- The frequency of fire ignition events can be described by a sigmoidally shaped probability distribution, fire occurs more frequently in natural grasslands than in shrubland.

- Fire spread is simulated as a spatially-explicit process. The fire spread algorithm is a simple version where five spreads across the stimulation landscape if neighbouring cells are combustible. Grasslands and shrublands differ in their ages of combustibility.

- In forests, the probability of tree mortality in disturbed sites is 1, since the disturbance is tree-felling. In grasslands and shrublands the probability of mortality for a tree in a burnt site depends on tree age and the level of disturbance.

- Human activities change the parameters of the prevailing disturbance regime. E.g., increased grazing intensity leads to more patchy fires.

Dispersal, seedling dynamics and recruitment:

- The recruitment capacity of a tree increases as a sigmoidal function of age.

- A tree's actual recruitment depends on when it last released a large seed load.

- We assume that wind is the only dispersal vector.

- Seedlings in unoccupied and disturbed sites recruit, i.e. we assume gap recruitment. The R-pine seedlings die if they fail to find a gap, whereas the U-pine seedlings only die if they are burnt.

Model implementation

- The program is initiated by simulating the disturbance regime for 100 years, thus allowing a distribution of vegetation ages characteristic of the disturbance regime to develop before the simulation of the invasion.

- The invasion process is done by setting up a plantation of adults trees adjacent to a block of natural vegetation (see above)

- Disturbance is the first model procedure, followed by mortality, dispersal, recruitment and age.

The qualitative predictions made by the model agree with the available data on the invasion of pines into forests, shrublands and grasslands. The outcome of the simulation runs clearly indicate that all factors considered (pine type, disturbance and environment) and all orders of interactions significantly influenced the rate of invasion. Most interestingly, many of the interactions had a greater effect than the main factors do. The authors suggest that such an integrative model is more suited as a predictive tool, because i) it also allows the prediction of the circumstances, i.e., the combination of factors, which facilitate or impede invasion, and ii) the mechanistic nature of the model allows the magnitude of the effects and interactive effects of these processes to be estimated.

5.3 Case study 3: Modelling the effect of changes in life-history traits on competitive ability of transgenic organisms

One of the risks of successful invasion is extinction of native species or genotypes. An increase in transgenic genotypes in a natural population is often assumed to be unlikely because transgenic organisms typically have some viability disadvantage. Muir and Howard (1999, 2001) examined the risk to a natural population after the release of a few transgenic individuals when the transgene traits simultaneously affects various life-history traits. They produced as a model a stock of transgenic Japanese medaka fish, *Oryzias latipes*, by inserting the human growth hormone gene (hGH), with a salmon promotor. Muir and Howard then conducted several experiments to document viability, development, fecundity and sexual selection of transgenic and wild-type medaka. A model was then developed to assess the consequences of the introduction of a small number of transgenic individuals into a large wild-type population. Different transgene lines are likely to vary in fitness even when the same transgene construct is used, because of differences in copy number and sites of transgene insertion. To take such variation into account as well as to make their model generally applicable to other organisms and transgene constructs, Muir and Howard used a range of parameter values for life-history traits.

The experiments conducted by Muir and Howard included experiments to assess the early viability of offspring produced from crosses involving transgenic and wild-type medaka parents. Results showed that early survival of transgenic young was 70% of that of wild type. In a mating experiment using wild-type medaka, mating advantage of large males over small males was shown. It was found that large males obtained a 4-fold mating advantage. Such size-related mating advantages have been demonstrated in a variety of fish species. Muir and Howard (1999) state that transgenic male medaka are not expected to have a mating advantage over wild-type males, because the hGH transgene which as inserted increased only juvenile growth rate, not final adult body size. Nonetheless, Muir and Howard modelled the possible effect of transgene release into wild-type populations when transgenes accelerate growth throughout adulthood, because these effects could occur with other transgene constructs in other fish species.

The deterministic model that was used assumes one locus with two alleles and predicts changes in population number and gene frequencies. The model is described in detail in Muir and Howard (1999).

Predictions of the model were straightforward when transgenes affected only one fitness component. If transgenes reduced only juvenile survival, transgenic individuals would be quickly eliminated from any wild-type population. In contrast, if the GH transgene increased only the mating success of transgenic males relative to wild-type males, the gene would spread quickly. Most interestingly, combining the effects of the transgene on mating success and offspring viability is predicted to result in the local extinction of any wild-type population invaded by transgenic organisms. The male mating advantage would act to increase the frequency of the transgene in the population; however, the viability disadvantage suffered by all offspring carrying the transgene would completely eliminate the population in a relatively low number of generations. Muir and Howard suggest that such risks should be evaluated with any new transgenic organism before release, and that their approach is well suited to do this.

6 Summary and Outlook

Predicting the risk of invasiveness by non-indigenous or genetically modified organisms is, and will continue to be, a challenge. In the past decades, considerable progress has been made in explaining and predicting plant invasions, but still very little is known for other groups of organisms.

6.1 Current knowledge in invasion ecology

The record of a plant's invasiveness in other geographic areas is currently the most reliable predictor of its ability to establish and invade new habitats. A number of species traits have been identified for plants that correlate with the likelihood of increased invasiveness, and these species traits have been repeatedly shown to explain fairly well why some plants have become invasive, and why other similar species haven't.

There are currently no broad scientific principles for identifying the invasive potential of plants or other organisms, but a conceptual basis exists for understanding invasions that can be developed into predictive principles. Various countries have already developed weed risk assessments systems, which are being used for predicting the risk of invasiveness of new deliberate introductions.

Unfortunately, these systems are still far from being accurate. The most likely reason for this is that invasiveness depends more upon the interaction between the characteristics of non-native species and their potential new habitats than upon the characteristics of the species alone. A promising approach may therefore be to develop systems or models that incorporate both species and habitat characteristics.

6.2 The search for characteristics that are negatively correlated with risk of invasion

Although it is important to identify characteristics significantly associated with an increased risk of invasion, it is equally important to identify characteristics that are unrelated, or even negatively correlated with risk of invasion. To date, no species traits have been found that are consistently unrelated to increased risk of establishment or invasion by non-indigenous organisms (Kolar and Lodge 2001).

The factors that are repeatedly used as indicators for low invasion risk are poor climate matching between the source and the new habitat, and the absence of hosts in the potential new habitat. Even though an unsuitable climate or the absence of known hosts are very good indicators for a low invasion risk, they do not stand for no risk at all. Populations of species introduced to new ranges have repeatedly been shown to evolve new traits that allow them to colonize areas with climatic conditions that populations from the native area cannot cope with (Hopper *et al*. 1993, Roy *et al*. 2000). Except for deliberate introduction of biological control agents, detailed information on the fundamental host-range (the range of hosts a species can complete its life-cycle) is often not known in detail, so a potential invader may start colonizing new hosts with which it has had no evolutionary past. Hence, one should be cautious in making predictions of the invasion risk of an organism solely on the fact that the potential new habitat has a unsuitable climate or no known hosts, but these two characteristics can and often are important integral parts of risk assessment systems.

6.3 Case studies to assess risk of increased invasiveness

Many ecologists believe that, by focusing on generalities, ecology as a science is and will not be able to provide good solutions to pressing environmental problems (Hansson 2003). Case studies on selected target species may therefore be more appropriate to assess the risks of increased invasiveness of a specific exotic or transgenic organism. Case studies combining field experiments carried out in different environments for several years and a modelling approach as presented in chapter 6 appear to be the most promising line of research.

Clearly, any models or predictive systems can only partially solve questions related to the risk of invasiveness of non-indigenous species or GMOs. Given the dependence of local population dynamics on local conditions, it has been suggested that models may best be used as frameworks in which to summarize experimental data. However, they are not machines for translating such data into confident predictions about a potential invader's ultimate success (Kareiva *et al.* 1996).

One other use of models may be to consult them for advice on how best to set up monitoring schemes. To some ecologists, this is the field where invasion theory can contribute most – not in predicting invasions, but in pinpointing the sampling programmes that would be most cost-effective at detecting a problem invasion before it is too late (Kareiva *et al.* 1996).

6.4 The inherent problem of pest risk assessment systems

One of the inherent problems of weed risk assessment systems is that the rate at which introduced species are converted to successful invaders is very low. Based on the tens rule, only some 0.1 % of the introduced species are expected to become pests. With such a low based rate, the damage caused by introducing a pest must be much higher than that caused by not introducing a harmless exotic or transgenic organism that is potentially useful (Smith *et al.* 1999).

However, the base-rate for the transition from naturalized to pest status is considerably higher (10% according to the tens rule). This raises the prospect that a national early warning system for invaders could focus much more reliably on picking the potential pests from amongst casual or naturalized species than from amongst imported species (Smith *et al.* 1999). As a sort of early warning system, Australian authorities have started to monitor populations of naturalized plant species that have a very high risk of becoming pests (A. Sheppard, personal comments).

6.5 Climate Change

Climate change may add an additional level of uncertainty to the prediction of future invasion events. In Europe, for example, winters are expected to become milder and summers hotter, and precipitation events less frequent but more intense by 2050 (IPCC 2001). There are several reasons to believe that invasive plant species will react differently to such changes than their native counterparts (Dukes and Mooney 1999), but there is still limited evidence to substantiate this. Plant species that have evolved under climatic conditions which are comparable to those predicted for a specific region may particularly profit from climate change. Rising atmospheric CO_2 might also positively affect establishment and population build-up of non-indigenous plant species. For example, growth of the non-indigenous evergreen woody plant *Prunus laurocerasus* significantly increased at an elevated CO_2 concentration compared to ambient CO_2, while the native *Ilex aquifolium*, with the same functional traits and similar life-history, showed no significant CO_2 response (Hättenschwiler and Körner 2003). Certainly, future invasion risk assessments need to consider climate change scenarios.

6.6 Outlook

One of the hopes of modern ecology is that the combination of experiments and models can solve many of our most challenging questions. Whether and how much models and short-term experiments can help in predicting invasion events remains open. However, there is a political and regulatory pressure on modern ecology to further improve the quality of predicting the risk of invasions. The problem is straightforward – handed a new organism, ecologists must quantify its invasiveness. Many promising new lines of research have been developed in the past few years, but it remains to be seen to what degree they will contribute to a more reliable prediction of the pest status of exotic or genetically modified organisms.

References

Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. Ecology Letters 6:712-715

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3:52-66

Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interaction. Science 301:1377-1380

Barrett SCH, Eckert GC, Husband BC (1993) Evolutionary processes in aquatic plants. Aquatic Botany 44:105-145

Baruch Z, Fernandez D (1993) Water relations of native and introduced C4 grasses in aneotropical savanna. Oecologia 96:179-185

Bergelson J (1994) Changes in fecundity do not predict invasiveness: A model study of transgenic plants. Ecology 75:249-252

Boudry PM, Morchen M, Saumitou-Laprade P, Vernet P, VAn Dijk H (1993) The origin and evolution of weed beets: consequences for the breeding and release of herbicide-resistant transgenic sugar beets. Theor. Appl. Genet. 87:471-478

Burke MJW, Grime JP (1996) An experimental study of plant community invasibility. Ecology 77:776-790

Callaway RM, Aschehoug ET (2000) Invasive Plants Versus Their New and Old Neighbors: A Mechanism for Exotic Invasion. Science 290:521-523

Callaway RM, Newingham B, Zabinski CA, Mahall BE (2001) Compensatory growth and competitive ability of an invasive weed are enhanced by soil fungi and native neighbours. Ecology Letters 4:429-433

Case TJ (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences 87:9610-9614

Case TJ (1991) Invasion resistance, species build up and community collapse in metapopulation models with interspecies competition. Biological Journal of the Linnean Society 42:239-266

Case TJ (1996) Global Patterns in the Establishment and Distribution of Exotic Birds. Biological Conservation 78:69-96

Chapman RM (1931) Animal Ecology with special reference to insects. McGraw-Hill, New York

Chittka L, Schürkens S (2001) Successful invasion of a floral market. Nature 411:653

Cleverly J, Smith S, Sala A, Devitt D (1997) Invasive capacity of *Tamarix ramosissima* in Mojave Desert floodplain: the role of drought. Oecologia 111:12-18

Cousens RD, Mortimer M (1995) Dynamics of weed populations. Cambridge University Press, Cambridge, U.K.

Copp GH, Garthwaite R, Gozlan RE (2003) A risk assessment protocol for freshwater fishes. In: www.aquatic-invasive-species-conference.org/ powerpoint_pdf/Session%20A/Thursday/ gordon_copp.pdf

Cowling RM, Pierce SM, Moll EJ (1986) Conservation and utilization of South Coast Renosterveld, an endangered South African vegetation type. Biological Conservation 37:363-377

Crawley MJ (1986) The population biology of invaders. Philos. Trans. R. Soc. London 314:711-731

Crawley MJ (1987) What makes a community invasible? In: Gray AJ, Crawley MJ, Edwards PJ (eds) Colonization, Succession & Stability. Blackwell Scientific Publications, Oxford, U.K., pp 429-453

Crawley MJ, Hails RS, Rees M, Kohn DD, Buxton J (1993) Ecology of transgenic oilseed rape in natural habitats. Nature 363:620-623

Cross J (1981) The establishment of *Rhododendron ponticum* in the Killarny Oakwoods, S.W. Ireland. Journal of Ecology 69:807-824

Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annual Review of Ecology and Systematics 34:183-211

D'Antonio CM, Dudley TL, Mack M, 1999 Disturbance and biological invasions: Direct effects and feedbacks. In: Walker LR (ed) Ecosystems of Disturbed Ground. Ecosystems of the World. Vol. 16. Elsevier Science, New York, pp 429-468

Davis AJ, Grime MA, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528-534

Davis MA, Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421-428

Déchamp C (1995) L'Ambroisie: un nouveau fléau. Edition Verso, Ahun

di Castri F, Hansen AJ, Debussche M, (eds) (1990) Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Press, Dordrecht, Boston, London

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14:135-139

Dukes JS (2001) Biodiversity and invasibility in grassland microcosms. Oecologia 126:563-568

Duncan RP (1997) The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. The American Naturalist 149:903-915

Duncan RP, Blackburn TM, Veltman CJ (1999) Determinants of geographical range sizes: a test using introduced New Zealand birds. J. Anim. Ecol. 68:963-975

Duncan RP, Bomford M, Forsyth D, Conibear L (2001) High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. Journal of Animal Ecology 70:601-632

Ehrlich PR (1989) Attributes of invaders and invading processes: Vertebrates. In: Drake J *et al*. (eds) Biological Invasions: A Global Perspective. John Wiley and Sons, New York, pp 315-328

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Chapman & Hall

Ghazoul J (2002) Flowers at the front line of invasion? Ecological Entomology 27:638-640

Goodwin BJ, McAllister AJ, Fahrig L (1999) Predicting invasiveness of plant species based on biological information. Conservation Biology 13:422-426

Goslee SC, Peters DPC, G BK (2001) Modeling invasive weeds in grasslands: the role of allelopathy in *Acroptilon repens* inavsion. Ecological Modeling 139:31-45

Green RE (1997) The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. Journal of Animal Ecology 66:25-35

Grevstad FS (1999) Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. Biological Invasions 1:313-323

Grotkopp E, Rejmanek M, Rost T (2002) Toward a Causal Explanation of Plant Invasiveness: Seedling Growth and Life-History Strategies of 29 Pine (Pinus) Species. The American Naturalist 159:396-419

Hättenschwiler S, Körner C (2003) Does elevated CO_2 facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests? Functional Ecology 17:778-785

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. The American Naturalist 94:421-425

Hansson L (2003) Why ecology fails at application: should we consider variability more than regularity? Oikos 100:624-627

Harrison S (1999) Local and regional diversity in a patchy landscape : native, alien and endemic herbs on serpentine. Ecology 80:70-80

Higgins SI, Richardson DM (1998) Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. Plant Ecology 135:79-93

Higgins SI, Richardson DM, Cowling RM (1996) Modeling invasive plant spread: The role of plant-environment interactions and model structure. Ecology 77:2043-2054

Hobbs RJ, Atkins L (1988) Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the western Australian wheat-belt. Australian Journal of Ecology 13:171-179

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity and invasion: implications for conservation. Conservation Biology 6:324-337

Holm LG, Plucknett DL, Pancho JV, Herberger JP (1991) The World's Worst Weeds: Distribution and Biology. Krieger Publishing Company, Melbourne, FL

Holway DA (1998) Simple rules for interspecific dominance in systems with exploitative and apparent competition. The American Naturalist 144:741-771

Hopper KR, Roush RT, Powell W (1993) Management of genetics of biological control introductions. Annu. Rev. Entomol 38:27-51

Huenneke L, Hamburg S, Koide R, Mooney HA, Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71:478-491

Hughes R, Vitousek PM, Tunison T (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. Ecology 72:743-746

Hunt CE, Behrens Yamada S (2003) Biotic resistance experienced by an invasive crustacean in a temperate estuary. Biological Invasions 5:33-43

IPCC (2001) Climate Change 2001: Synthesis Report. A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Integovernmental Panel on Climate Change [Watson, R.T. and the Core Writing Team (eds.)]. Cambridge University Press, Cambridge,United Kingdom, and New York, NY, USA, 398 pp.

Kareiva P, Parker IM, Pascual M (1996) Can we use experiments and models in predicting the invasiveness of genetically engineered organisms? Ecology 77:1670-1675

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17:164-170

Kennedy T, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636-638

Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417:67-70

Knops JMH, Tilman D, Haddad NM, et_al. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecology Letters 2:286-293

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol. Evol. 16:199-204

Kowarik I (1995a) Time lags in biological invasions with regard to the success and failure of alien species. In: Pysek P, Prach K, Rejmanek M, Wade PM (eds) Plant Invasions. SPB Academic Publishing, The Hague, The Netherlands, pp 15-38

Kowarik I (1995b) On the role of alien species in urban flora and vegetation. In: Pysek P, Prach K, Rejmanek M, Wade PM (eds) Plant Invasions. SPB Academic Publishing, The Hague, The Netherlands, pp 85-103

Kowarik (2003) Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa. Verlag Eugen Ulmer, Stuttgart, Germany

Kruess A, Tscharntke T (1994) Habitat fragmentation, species loss, and biological control. Science 264:1581-1584

Krysan JL, Miller TA (1986) Methods for Study of Pest Diabrotica. Springer Verlag, New York, USA

Lee CE (2002) Evolutionary genetics of invasive species. Trends Ecol. Evol. 17:386-391

Levine JM, Kennedy T, Naeem S (2002) Neighbourhood scale effects of species diversity on biological invasions and their relationship to community patterns. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, New York , pp 114-124

Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. Science 288:852-854

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15-26

Linder CR, Schmitt J (1995) Potential persistence of escaped transgenes: Performance of transgenic, oil-modified Brassica seeds and seedlings. Ecological Applications 5:1056-1068

Lonsdale WM (1993) Rates of spread of an invading species - *Mimosa pigra* in northern Australia. Journal of Ecology 81:513-521

Lonsdale WM (1994) Inviting trouble: Introduced pasture species in northern Australia. Australian Journal of Ecology 19:345-354

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522-1534

Lonsdale WM, Braithwaite R (1988) The shrub that conquered the bush. New Scientist 120:52-55

Loope LL, Mueller-Dombois D (1989) Characteristics of invaded islands, with special reference to Hawaii. In: Drake JA, Mooney HA, di Castri F, *et al*. (eds) Biological Invasions: A Global Perspective. Wiley, Chichester, pp 257-280

Lyons K, Schwartz M (2001) Rare species loss alters ecosystem function - invasion resistance. Ecology Letters 4:358-365

Mack RN (1989) Temperate grasslands vulnerable to plant invasions: characteristics and consequences. In: Drake J *et al*. (eds) Biological Invasions: A Global Perspective. John Wiley, Chichester, UK, pp 155-179

Mack RN, Thompson JN (1982) Evolution in steppe with few, large, hooved mammals. The American Naturalist 119:757-773

Marler M, Zabinski C, Callaway RM (1999) Mycorrhizae indirectly enhance competitive effects of an invasive form on a native bunchgrass. Ecology 80:1180-1186

Maron J, Jefferies R (1999) Bush lupine mortality, altered resource availability and alternative vegetation states. Ecology 80:443-454

Matthews RA (1996) Base-rate errors and rain forecasts. Nature 382:766

Matthews RAJ (1997) Decision-theoretic limits on earthquake prediction. Geophysics Journal International 131:526-529

McLain DK, Moulton MP, Redfearn TP (1995) Sexual selection and the risk of extinction of introduced birds on oceanic islands. Oikos 74:27-34

McMillan M, Wilcove D (1994) Gone but not forgotten: why have species protected by the Endangered Species Act become extinct? Endangered Species Update 11:5-6

Meekins JF, McCarthy BC (2001) Effects of environmental variations on the invasive success of an non-indigenous forest herb. Ecological Applications 11:1336-1348

Meinesz A (1999) Killer algae. University of Chicago Press, Chicago, IL

Memmott J, Fowler SV, Hill RL (1998) The effect of release size on the probability of establishment of biological control agents: gorse thrips (*Sericothrips staphylinus*) released against gorse (*Ulex europaeus*) in New Zealand. Biocontrol Science and technology 8:103-115

Menges E (1990) Population viability for an endangered plant species. Conservation biology 4:41-62

Menges E (1991) The application of minimum viable population theory to plants. In: Falk DA, Holsinger KE (eds) Genetics and Conservation of Rare Plants. Oxford University Press, New York, pp 45-61

Menges E (1992) Stochastic modeling of extinction in plant populations. In: Fiedler PL, Jain SK (eds) Conservation Biology. Oxford University Press, New York, pp 253-275

Milchunas DG, Lauenroth WK (1995) Inertia in plant community structure: state changes after cessation of nutient-enrichment stress. Ecological Applications 5:452-458

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625-627

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. PNAS 98:5446-5451

Morgan J (1998) Patterns of invasion of an urban remnant of an species-rich grassland in southeastern Australia by non-native plant species. Journal of Vegetation Science 9:181-190

Moulton MP, Pimm SL (1983) The introduced Hawaiian avifauna: biogeographic evidence for competition. The American Naturalist 121:669-690

Mücher T, Hesse P, Pohl-Orf M, Ellstrand NC, Bartsch B (2000) Characterization of weed beet in Germany and Italy. Journal of Sugar Beet Research 3:19-38

Muir WM, Howard RD (1999) Possible ecological risks of transgenetic organism release when transgenes affect mating success: Sexual selection and the Trojan gene hypothesis. PNAS 96:13853-13856

Muir WM, Howard RD (2001) Fitness Components and Ecological Risk of Transgenetic Release: A Model Using Japanese Medaka (*Oryzias latipes*). The American Naturalist 158:1-16

Mueller H, Nuessly GS, Goeden RD (1990) Natural enemies and host-plant asynchrony contributing to the failure of the introduced moth, *Coleophora parthenica* Meyerick (Lepidoptera: Coleophoridae), to control Russian thistle. Agriculture, Ecosystems & Environment 32:133-142

Mueller-Scharer H, Steinger T (2003) Predicting evolutionary change in invasive, exotic plants and its consequences for plant-herbivore interactions. In: Ehlers LE, Sforza R, Mateille R (eds) Genetics, Evolution and Biological Control. CABI Publishing, Wallingford, pp 137-162

Naeem S, Knops J, Tilman D, Howe K, Kennedy T, Gale S (2000) Plant diversity increases resistance to invasion in the absence of co-varying extrinsic factors. Oikos 91:97-108

National Academy of Sciences (2002) Predicting invasions of non-indigenous plants and plant pests. National Academy Press, Washington, D.C.

Newsome AE, Noble IR (1986) Ecological and physical characters of invading species. Cambridge University Press

Niemelä P, Mattson WJ (1996) Invasion of North American forests by European phytophagous insects. BioScience 46:741-753

O'Connor RJ (1986) Biological characteristics of invaders among bird species in Britain. Philos. Trans. R. Soc. London Ser. B314:583-598

Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404:278-281

Palmer M, Maurer T (1997) Does diversity beget diversity? A case study of crops and weeds. Vegetation Science 8:235-240

Pannel JR, Barrett SCH (1998) Baker's Law revisited: reproductive asurance in a metapopulation. Evolution 52:657-668

Pemberton RW (2000) Naturalization patterns of horticultural plants in Florida. In: Spencer NR (ed), Proceedings of the 10th International Symposium on Biological Control of Weeds. Montana State University, Bozeman, Montana, USA, p 881

Perrins J, Williamson M, Fitter A (1992) Do annual weeds have predictible characteristics. Acta Oecologica 13:517-533

Pessel FD, Lecomte J, Emeriau V, Krouti M, Messean A, Gouyon PH (2001) Persistence of oilseed rape (*Brassica napus* L.) outside of cultivated fields. Theoretical and Applied Genetics 102:841-846

Pheloung P (1995) Determining the weed potential of new plant introductions to Australia. In: Agriculture Protection Board Report, West Australian Department of Agriculture, Perth, Western Australia, p 26 pp

Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs associated with non-indigenous species in the United States. BioScience 50:53-65

Porter SD, Savignano DA (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71:2095-2106

Prieur-Richard A, Lavorel S, Linhart YB, Santos Ad (2001) Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. Oecologia 130:96-104

Pysek P (1998) Alien and native species in Central European urban floras: a quantitative comparison. Journal of Biogeography 25:155-163

Pysek P, Prach K, Smilauer P (1995) Relating Invasion Success to Plant Traits: An Analysis of the Czech Alien Flora. In: Pysek P, Prach K, Rejmanek M, Wade PM (eds) Plant Invasions. SPB Academic Publishing, The Hague, The Netherlands, pp 39-60

Reichard SH (1997) Prevention of invasive plant introduction on national and local levels. In: Luken JA, Thieret JA (eds) Assessment and Management of Plant Invasions. Springer-Verlag, New York, pp 215-227

Reichard SH (2001) The search for patterns that enable invasion predictions. IN: Groves RH, Panetta FR, Virtue JG (eds), Weed risk assessment. CSIRO, Melbourne, Australia, pp 10-19

Reichard SH, Hamilton CW (1997) Predicting invasions of woody plants introduced into North America. Conservation Biology 11:193-203

Rejmanek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655-1661

Ricciardi A, Whoriskey F, Rasmussen J (1997) The role of zebra mussel (*Dreissena polymorpha*) in structuring macro-invertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Sciences 67:613-619

Richardson DM, Cowling RM, Le Maitre DC (1990) Assessing the risk of invasive success in *Pinus* and *Banksia* in South African mountain fynbos. Journal of Vegetation Science 1:629-642

Richardson DM, MacDonald IAW, Forsyth GG (1989) Reductions in plant species richness under stands of alien trees and shrubs in the Fynbos biome. South African Forestry Journal 149:1-8

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93-107

Ridenour WM, Callaway RM (2001) The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126:444-450

Robinson G, Quinn J, Stanton M (1995) Invasibility of experimental habitat islands in a Californian annual winter grassland. Ecology 76:786-794

Roy J, Simon J-P, Lapointe F-J (2000) Determination of the origin of the cold-adapted populations of barnyard grass (*Echinochloa crus-galli*) in eastern North America: a total-evidence approach using RAPD DNA and DNA sequences. Canadian Journal of Botany 78:1505-1513

Roy J, Navas ML, Sonie L, Alpert P (1992) Invasion of Mediterranean-type regions by annual species of *Bromus*. In: Conesa JA, Recasens J (eds) Actes dei Simposi Internacional de Botanica Pius Font i Quer, 1988. Institut d'Estudis Ilerdencs, Lleida, pp 389-393

Schaffner U (2001) Host range testing of insects for biological weed control: how can it be better interpreted? BioScience 51:1-9

Scott JK, Panetta FD (1993) Predicting the Australian weed status of southern African plants. Journal of Biogeography 20:87-93

Simberloff D, Von Holle B (1999) Positive interactions of non-indigenous species: invasional meltdown? Biological Invasions 1:21-32

Smith CS, Lonsdale WM, Fortune J (1999) When to ignore advice: invasion prediction and decision theory. Biological Invasions 1:89-96

Snow AA , Pilson D, Rieseberg LH *et al.* (2003) A Bt transgene reduces herbivory and enhances fecundity in wild sunflowers. Ecological Applications 13:279-286

Sol D, Lefebvre L (2000) Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90:599-605

Sorci G, Moller AP, Clobert J (1998) Plumage dichromatism of birds predicts introduction success in New Zealand. Journal of Animal Ecology 67:263-269

Stachowicz JJ, Withlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286:1577-1579

Stachowicz JJ, Fried H, Withlatch RB, Osman RW (2002) Biodiversity, invasion resistance and marine ecosystem function: reconciling pattern and process. Ecology 83:2575-2590

Stermitz FR, Bais HP, Foderaro TA, Vivanco JM (2003) 7,8- Benzoflavone: a phytotoxin from root exudates of invasive Russian knapweed. Phytochemistry 64:493-497

Stohlgren T, Otsuki Y, Villa CA *et al.* (1999) Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25-46

Sun M, Corke H (1992) Population genetics of colonizing success of weedy rye in northern California. Theoretical and Applied Genetics. 88

Suneson CA, Rachie KO, Kush GS (1969) A dynamic population of weedy rye. Crop Science 9:121-124

Symstad A (2000) A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81:99-109

Thompson K, Hodgson JG, Grime JP, Burke MJW (2001) Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. Journal of Ecology 89:1054-1060

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81-92

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421:628-630

Tsutsui ND, Suarez AV, Holway DA, Case TJ (2000) Reduced genetic variation and the success of an invasive species. Proceedings of the National Academy of Sciences 97:5948-5953

US Department of Agriculture (2000) National Tour to Highlight Non-native, Invasive Pests and Diseases That Threaten American Agriculture and National Resourses. Press Release No. 0085.00

van der Putten WH, van Dijk C, Peters BAM (1993) Plant-specific soil-borne diseases contribute to succession in foredune vegetation. Nature 362:53-56

van der Putten WH, Mortimer SR, Hedlund K, van Dijk C, Brown VK, Leps J, Rodriguez-Barrueco C, Roy J, Diaz Len TA, Gormsen D, Korthals GW, Lavorel S, Santa Regina I, Smilauer P (2000) Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. Oecologia 124:91-99

Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. The American Naturalist 147:542-557

Vitousek PM, Walker LR (1989) Biological invasion by *Myrica faya* in Hawaii: Plant demography, nitrogen fixation ecosystem effects. Ecological Monographs 59:247-265

Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802-804

Wardle DA (2001) Experimental demonstration that plant diversity reduces invasibility - evidence of a biological mechanisms or a consequence of sampling effect? Oikos 95:161-170

Weber E, Schmid B (1998) Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. American Journal of Botany 85:1110-1121

Wedin D, Tilman D (1993) Competition among grasses along a nitrogen gradient: Initial conditions and mechanisms of competition. Ecological Monographs 63:199-229

White T, Campbell B, Kemp P (1997) Invasion of temperate grassland by the a subtropical annual grass across an experimental matrix of water stress and disturbance. Journal of Vegetation Science 8:847-854

Wilcove DS, Rothstein D, Dubow J, Phillips E, Losos E (1998) Quantifying threats to imperiled species in the United States. BioScience 48:607-615

Williams DG, Baruch Z (2000) African grass invasion in the Americas: ecosystems consequences and the role of ecophysiology. Biological Invasions 2:123-140

Williamson M (1996) Biological Invasions. Chapman & Hall, London, UK

Williamson M (1999) Invasions. Ecography 22:5-12

Williamson M, Fitter A (1996) The varying success of invaders. Ecology 77:1661-1666

Wittenberg R, Cock M, (eds) (2001) Invasive Alien Species: A Tool Kit of Best Prevention and Management Practices. CAB International, Wallingford, Oxon, UK

Appendices

Appendix 1:	**Characteristics of habitats and risk of invasibility**
Appendix 2:	**Characteristics of release events and risk of invasion**
Appendix 3:	**Characteristics of species and risk of invasiveness**
Appendix 4:	**Explanatory and predictive power of multi-species studies assessing the risk of increased invasiveness**

Appendix 1. Characteristics of habitats that are either positively or negatively associated with establishment and invasion of exotic alien species.

	Establishment		Invasion		
Characteristics	Plants	Animals	Plants	Animals	References
(Change in) Disturbance	+,		+,+,+,+,+	Ns	8,10,16,18,38,40-41
Long history of human disturbance	-,-,-		+		1-2,8,42
High species richness	-,+,-,-,ns,-,+,-,-	+	-,-,+,-,-,ns,-,-	Ns	3,6-7,16-17,24-25,27-28,31,33-35,39
Interspecific competition	-,-				54-55
Presence of other exotic species	+		+,+,+,+	+	8-12,
Presence of antagonists	-		-,-	-,-	19-20,37,50
Presence of mutualists			+,+,+,+,+		13-14,21-23
Habitat fragmentation	+				15
Nutrient availability	+		+,+,+,+,+,+		15,18,41,43-44,46,48
Water availability	+		+,+,+,-		29-30,45,49
Light availability	+				36

References:

1) Roy *et al.* (1992), 2) Lonsdale (1999), 3) Tilman (1997), 4) Case (1990), 5) Case (1991), 6) Stohlgren *et al.*(1999), 7) Levine and D'Antonio (1999), 8) Mack and Thompson (1982), 9) Lonsdale and Braithewaite (1988), 10) Cross (1981), 11) Ricciardi *et al.* (1997), 12) Hughes *et al.* (1991), 13) Marler *et al.* (1999), 14) Richardson *et al.* (2000), 15) Harrison (1999), 16) Holway (1998), 17) Stachowicz *et al.* (1999/2002), 18) Thompson *et al.* (2001), 19) Prieur-Richard *et al.* (2002), 20) Hunt *et al.*(2003), 21) Callaway *et al.* (2001), 22) Chittka and Schürkens (2001), 23) Ghazoul (2002), 24) van der Putten *et al.* (2000), 25) Lyons and Schwartz (2001), 26) Palmer and Maurer (1997), 27) Robinson *et al.* (1995), 28) Naeem *et al.* (2000), 29) White *et al.* (1997), 30) Cleverly *et al.*. (1997), 31) Levine (2000), 32) Wardle (2001), 33) Symstad (2000), 34) Dukes (2001), 35) Knops *et al.* (1999), 36) Meekins and McCarthy (2001), 37) Klironomos (2002), 38) Kowarik (1995b), 39) Kennedy *et al.* (2002), 40) Cowling *et al.* (1986), 41) Burke and Grime (1996), 42) Hobbs and Huenneke (1992), 43) Huenneke *et al.* (1990), 44) Hobbs and Atkins (1988), 45) Davis and Pelsor (2001), 46) Baruch and Fernandez (1993), 47) Morgan (1998), 48) Maron and Jefferies (1999), 49) Milchunas and Lauenroth (1995), 50) Mueller *et al.* (1990)

Appendix 2. Relationship between characteristics of release events and completion of invasion transition (modified from Kolar and Lodge, 2001).

	Establishment	Invasion		
Characteristics	Animals	Plants	Animals	References
● Number of individuals released	+,+,+,+,+,+,+,+,+		+,+,+	6,7,8,9,10,15,18, 19,20
● Number of introduction attempts	+,+,+,+,+,Ns,Ns		+	6,9,19,15,18,21
● Time since introduction	+,-,Ns	-	Ns	6,7,10,11,18

References:
6) Duncan *et al*. (1999), 7) Newsome and Noble (1986), 8) O'Connor (1986), 9) Veltman *et al.* (1996), 10) Green (1997), 11) Scott and Panetta (1993), 15) Sorci *et al.* (1998), 18) Duncan (1997), 19) Grevstad (1999), 20) Memmott *et al.* (1998), 21) Case (1996)

Appendix 3. Characteristics of species that are either positively or negatively associated with establishment and invasion (modified from Kolar and Lodge, 2001).

* Categorial variable with significant relationship between variable and transition completion

	Establishment		Invasion		
Characteristics	Plants	Animals	Plants	Animals	References
Vegetative reproduction			+,+,+		1, 2
Behavioral plasticity		+			3
Sexual selection		-			4
Number of offspring		+,-,Ns,Ns	+	+	2,5,6,7,8,9
Offspring mass			Ns,Ns,Ns,Ns,-,-	-	2,5,10,11,12
Broods per season		+,Ns		+	5,7,8
Dispersal mechanism			Ns,Ns,Ns,+,+		1,2,15
Length of juvenile period			Ns,Ns,-,-,-	-	1,2,5,12
Flowering period	+		+,+		1,13
Body mass		+,+,Ns,Ns,Ns		-	5,8,9,14
Size	+	Ns	+,Ns,Ns,		1,8,11,12,13
Longevity			Ns,Ns,	+	5,12
History of invasion			+,+,+,+		1,2,10
Origin	*	*,*	*,*,Ns		1,6,9,11,15
Range area	+	Ns,Ns	+,Ns		1,8,10,13,16
Family or genus invasive			+,+,+,+		1,10,

References:
1) Reichhard and Hamilton (1997), 2) Richardson *et al.* (1990), 3) Sol and Lefebvre (2000), 4) McLain *et al.* (1995), 5) Duncan *et al.* (1999), 7) Newsome and Noble (1986), 8) O'Connor (1986), 9) Veltman *et al.* (1996), 10) Green (1997), 11) Scott and Panetta (1993), 12) Lonsdale (1994), 13) Rejmanek and Richardson (1996), 14) Goodwin *et al.* (1999), 15) Sorci *et al.* (1998), 16) Pysek (1998), 17) Williamson and Fitter (1996)

Appendix 4. Explanatory and Predictive power found in multi-species comparison studies

Authors	**Organisms**	**Statistics**	**Significant traits**	**Explanatory power**	**Predictive power**
Perrins *et al.* (1992)	Annual plants				78%
Scott and Panetta (1993)	Plants	Multiple log. regression	South African climates, congeneric weeds	40% of variance explained	
Phaloung (1995)	Plants	qualitative			66-85%
Case (1996)	Birds	stepwise regression	Area, introductions, number of endemics	65.5% of variance explained	
Veltman *et al.* (1996)	Birds	Multiple log. regression	No. of propagules, migration, body mass, insect months	total model 53,5%, significant parameter 26,2% of variance	
Rejmanek and Richardson (1996)	Pines	Discriminant analysis	Seed mass, interval between large seed crops, min. juvenile period	77,8% of variance, 100% correctly classified	
Duncan (1997)	Birds	Multiple log. regression	No. of indviduals released, No. of species present	47,3% of deviance	

Green (1997)	Birds	Log. regression	No. of individuals released, body weight, clutch size		
Reichard and Hamilton (1997)	Woody plants	Discriminant analysis	leaves evergreen, invaders elsewhere, vegetative reproduction, flowers perfect, flowers in winter, length of time fruit is on plant, no seed pretreatment, Cold needed for seed germination, native to temperate Asia, native to N. America, intraspecific hybrids,	67% of variance explained	Total 86.2% correctly classified (97,1% invaders, 29.2% of non-invaders
Sorci *et al.* (1998)	Birds	Multiple log. regression	no. of released individuals, plumage dichromatism		
Duncan *et al.* (1999)	Birds	multiple regression	broods per season, mitratory tendency, no. of individuals released	80% of variance explained	
Goodwin *et al.* 1999	Plants	Multiple log. regression	stem height, flowering period	68.3% of variance explained	61.8% correctly classified (61.8% each of invaders and non-invaders)

Goodwin et al. 1999	Plants	Multiple log. regression	range	88.2% of variance explained	71.8% correctly classified (70.9% of invaders, 72.7% of non-invaders)
Duncan et al. (2001)	Birds	multiple log. regression	No. of introductions, gamebird, climate matching, introduced successfully elsewhere, body mass	68.3% of deviance explained	
Weber and Gut (unpubl)	Plants	qualitative			64.4% correctly classified, (76.6% of invaders, 61.6% of non-invaders)