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Colin R. Townsend obtained his B.Sc. and Ph.D. degrees from the University of Sussex. His previous teaching appointments have been in the Animal Ecology Research Group of Oxford University's Zoology Department and in the School of Biological Sciences at the University of East Anglia. Currently he is Professor and Head of Department of Zoology at the University of Otago. His teaching interests encompass general ecology, wildlife management and aquatic ecology. He is joint author of the textbook Ecology: Individuals, populations and communities (Begon, Harper and Townsend).

In England, Colin's research concerned the ecology of streams and shallow lakes, with emphasis on the role of predation in structuring aquatic communities. The Taieri River Project now takes up most of his research time. This is aimed at understanding the impact of introduced brown trout on New Zealand's native biota, the role that land use plays in stream ecology, and the relative importance of biotic factors and physical disturbance in determining the nature of stream communities.

EXOTIC SPECIES MANAGEMENT AND THE NEED FOR A THEORY OF INVASION ECOLOGY

The popular concept of nature in balance, of natural communities as ancient, co-evolved assemblages is wrong in many, perhaps most, cases. Contemporary native communities are periodically exposed to exotic species arriving under their own steam, some to fail, some to establish without much impact, others no doubt to wreak formidable change. A longer-term perspective is provided by palaeoecologists who describe a continuous process of community reassembly as species shift in different directions, at different rates, during different times in response to climatic and environmental changes (Graham, 1988).

Against this background of natural change, human actions have caused the comparative trickle of exotic species to be replaced by a flood, much to the consternation of conservation-minded people. Yet we are woefully ignorant of what determines whether an introduced species will establish, and which species we need to be particularly concerned about because of a propensity to cause significant change. Despite many calls for research, funds are not usually forthcoming for the 'luxury' of investigations of introduced species that have no likelihood of removal - studies which can be viewed as providing information 'only for the eulogy' (Coblentz, 1990).

However, understanding of the reasons for successful establishment and spread of introduced species is vital if we are to make better decisions in future. Such knowledge can be used in two ways;

on the one hand, to deal with specific problems concerning the species in question and, on the other, to develop general theories about the characteristics of species that are likely to be successful colonists and/or damaging to the community that receives them. I will deal with specific and general cases in turn.

There is no more valuable information in the search for a promising biocontrol agent than the description of a successful introduction in another part of the world. However, it is not enough simply to know that an economic gain has been made in the battle against the pest. Reassurance that the control agent will 'work' in the new location is also needed and, even more important, that the introduced species will not have unacceptable effects on non-target species. Only if research has been carried out can a reasonable evaluation of likely benefits and risks be made. Consideration of proposals to introduce food species will also benefit if introductions elsewhere have been properly monitored. A topical case in New Zealand concerns the channel catfish (*Ictalurus punctatus*), a fish that has been introduced to many countries around the world in attempts to emulate the successful aquaculture industry in the southern United States. Our assessment of the risks posed after escape from aquaculture facilities was hampered by the apparent lack of data about its impact as an exotic elsewhere in the world. Fortunately, the results of some research were uncovered (rather late in the

process) and these revealed a likely adverse effect on a variety of valued New Zealand species (Townsend and Winterbourn, 1990).

Planning for global climatic change also requires species-specific information. What will happen if native plants and animals begin to move in reaction to warming climates - will our biological reserves turn out to be in the wrong places (Peters and Darling, 1985)? Even in an untouched landscape, some species would have trouble keeping up with the predicted 'greenhouse' warming but surrounded by a sea of exotic competitors and predators their chances of unassisted movement to appropriate new habitats must be remote indeed (McGlone, Clarkson and Fitzharris, 1990). To compound the problem further, successful exotic species might become even more successful in the changing world. It is important to be able to predict the likely consequences of warming for the distribution of exotics and natives and to take what action is necessary, even to the extent of planning new reserves to which endangered natives can be shifted at an appropriate time. One particularly extreme scenario has rare mammals, such as cheetahs and rhinoceroses, transplanted to the American southwest as their African habitats continue to be usurped - is this a mad scientist's dream, or a realistic crisis move which, after all, would serve to restore a semblance of the Nearctic palaeomammalian megafauna lost a few thousand years ago (Soulé, 1990)?

Turning now to the need to develop general theory, it is clear that our understanding of the invasion process is rudimentary (Crawley, 1986). However, we know that some traits may predispose invading species to successful establishment - high reproductive rate, short generation time, long-range dispersal ability, phenotypic plasticity, generalist diet, broad physical tolerance range and local absence of enemies. (Note that some of these also define ruderal and super-tramp species.) Prediction of likely ecological impact is more problematic - the lack of reliable forecasting rules is well illustrated by the strikingly different effects that apparently similar species can have (e.g., the house sparrow and tree sparrow, *Passer domesticus* and *P. montanus*, in North America; Simberloff, 1990). While direct effects of an invader on residents via predation, herbivory, competition or disease-transmission may not be too difficult to guess, there is little basis for predicting subtle knock-on effects or deciding whether an invader may turn out to be a 'keystone' species with a widespread impact. Finally, we are equally poorly informed about the characteristics of natives that render

them more or less vulnerable and the features of the environment that may serve to exaggerate or ameliorate the impact of an exotic (though habitats disturbed by human action seem often to be particularly vulnerable to invasions by plants and animals).

A general theory of invasion ecology needs to be developed for a number of reasons. For one thing, it would provide for the prediction of risks and benefits of a potential biocontrol agent, even in the absence of species-specific information about success elsewhere. Similarly, a basis would be provided for evaluating the risks associated with introduction of species for enterprises such as aquaculture or horticulture. Less obviously, future decisions to release genetically engineered microbes, plants or animals would be able to take into account predictions about their impact as invaders (Miller, 1991). Finally, such a theory is crucial to future conservation effort.

We must move forward on two fronts. The literature on introduced organisms, biocontrol and theoretical ecology needs to be scanned and synthesized in a search for predictors of environmental impact. This process must also tap the unpublished knowledge of successes and failures in biocontrol, aquaculture and other programmes of planned introductions. New Zealand's Ministry for Environment is currently involved in drawing up new policy for assessing import proposals and is wisely sponsoring research that aims both at synthesis and at *post-hoc* investigations of successful invaders to determine whether their adverse effects could have been predicted. Any 'rules of thumb' that emerge can be used to decide whether a fast or slow-track protocol should be met for specific import applications. The other requirement for the future is a higher priority for research on species as they invade and spread through a landscape. If such work had been done in the past we would now be closer to the goal of a theory of invasion ecology.

Homogenization of ecological communities by the world-wide spread of exotics does present a gloomy prospect but we need to remain vigilant in our attempts to prevent the introduction of further undesirable aliens and to control aggressive exotics that have already arrived. However, ecologists should also look ahead and begin to take up the challenge of managing the novel biogeographical assemblages with which we are confronted. Perhaps a sister-discipline for 'restoration ecology' will emerge, to be called 'recombination ecology', as we start to consider the relative merits of artificial as opposed to natural assemblages for the maintenance of biodiversity (Soulé, 1990).

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