

The local introduction of strongly interacting species and the loss of geographic variation in species and species interactions

CRAIG W. BENKMAN,* ADAM M. SIEPIELSKI* and THOMAS L. PARCHMAN*†

*Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA, †Department of Biology, MSC 3AF, New Mexico State University, Las Cruces, NM 88003, USA

Abstract

Species introductions into nearby communities may seem innocuous, however, these introductions, like long-distance introductions (e.g. trans- and intercontinental), can cause extinctions and alter the evolutionary trajectories of remaining community members. These 'local introductions' can also more cryptically homogenize formerly distinct populations within a species. We focus on several characteristics and the potential consequences of local introductions. First, local introductions are commonly successful because the species being introduced is compatible with existing abiotic and biotic conditions; many nearby communities differ because of historical factors and the absence of certain species is simply the result of barriers to dispersal. Moreover, the species with which they interact most strongly (e.g. prey) may have, for example, lost defences making the establishment even more likely. The loss or absence of defences is especially likely when the absent species is a strongly interacting species, which we argue often includes mammals in terrestrial communities. Second, the effects of the introduction may be difficult to detect because the community is likely to converge onto nearby communities that naturally have the introduced species (hence the perceived innocuousness). This homogenization of formerly distinct populations eliminates the geographic diversity of species interactions and the geographic potential for speciation, and reduces regional species diversity. We illustrate these ideas by focusing on the introduction of tree squirrels into formerly squirrel-less forest patches. Such introductions have eliminated incipient species of crossbills (*Loxia* spp.) co-evolving in arms races with conifers and will likely have considerable impacts on community structure and ecosystem processes.

Keywords: co-evolution, divergent selection, geographic selection mosaic, keystone species, *Loxia*, strongly interacting species

Received 8 February 2007; revision accepted 27 March 2007

Introduction

Islands are the source of many new species (Mayr 1963). One reason is that gene flow is interrupted between populations on different islands. However, intervening water barriers are more than just barriers to gene flow. They differentially affect the ability of different species to colonize islands, which result in islands differing both

from each other and from the mainland in their biotic compositions. Of course, islands may also differ in abiotic conditions, and this further compounds the biotic variation that drives divergent selection between populations. Conversely, the varying biotic compositions and especially the absence of certain species from islands (e.g. large mammalian predators and herbivores) make them particularly vulnerable to devastating impacts from species introductions (Blackburn *et al.* 2004; Cox & Lima 2006). Thus, the threat of introductions to biota of isolated islands is rightfully the concern of many conservation biologists. Another major concern of conservation biologists is the

Correspondence: Craig W. Benkman, Fax: 307-766-5625; E-mail: cbenkman@uwyo.edu

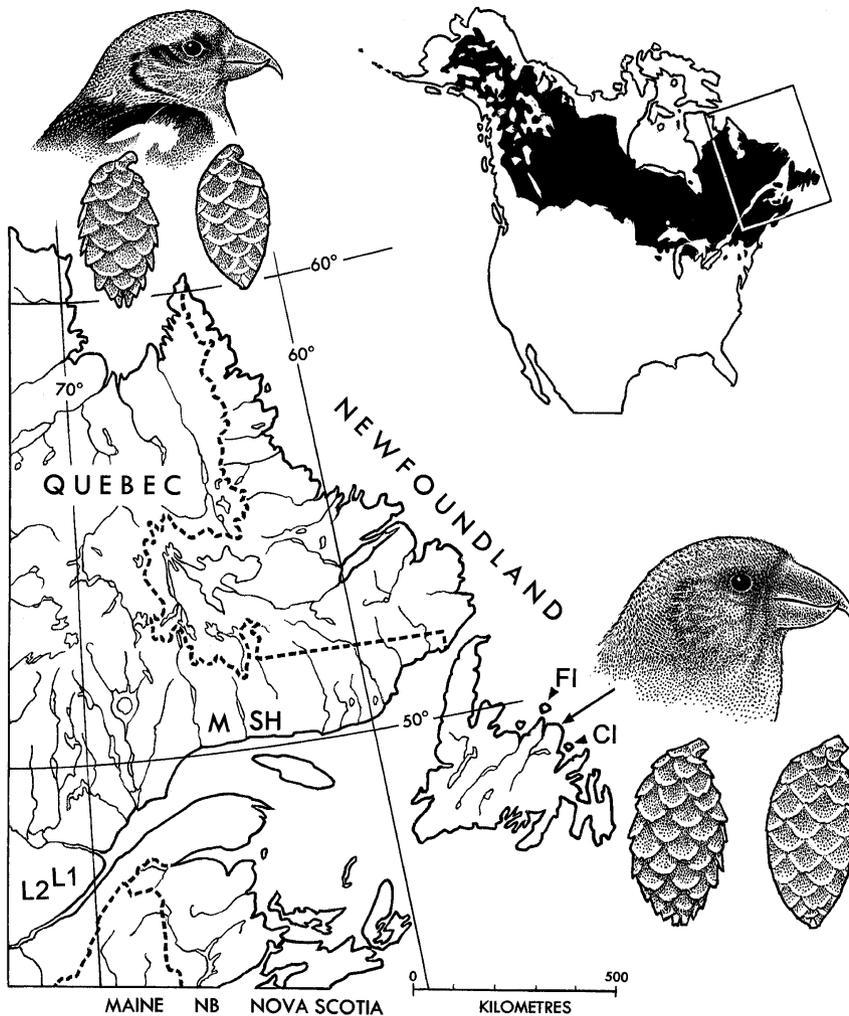


Fig. 1 The distribution of black spruce (*Picea mariana*) (black) in the map in the upper right, a white-winged crossbill (*Loxia leucoptera leucoptera*) (upper left) and a Newfoundland crossbill (*Loxia curvirostra percna*) (lower right), and representative partially closed and closed black spruce cones from the mainland (upper left) and Newfoundland (lower right). Red squirrels *Tamiasciurus hudsonicus* occur throughout the spruce forests of the mainland and were introduced onto Newfoundland in 1963. Black spruce on Newfoundland has lost defences directed at squirrels (e.g. the ratio of cone mass to seed mass is lower on Newfoundland than on the mainland) while increasing defences directed at crossbills (e.g. thicker scales on Newfoundland than on the mainland). From Parchman & Benkman (2002).

impacts stemming from trans- and intercontinental species introductions.

While the consequences of such introductions are clearly important (Mack *et al.* 2000), we would like to focus on how local introductions cause extinctions and eliminate divergent selection between populations and thus erode processes that give rise to diversity. By 'local introductions', we mean introductions of species into nearby habitats that are otherwise quite similar to their source habitat. We start with examples from our research. Throughout, we place an emphasis on the importance of considering the conservation and maintenance of the geographic diversity of interactions among species rather than merely species themselves (Thompson 2005).

Years ago, one of us visited Newfoundland in an effort to understand the factors contributing to the adaptive radiation of crossbills (*Loxia*), a genus of finches that is specialized for foraging on seeds in conifer cones. The conifer forests of Newfoundland appeared quite similar to those on the nearby mainland of North America (separated

by as little as 15 km), yet, perplexingly, the endemic and large-billed Newfoundland crossbill (*Loxia curvirostra percna*) was remarkably distinct from crossbills on the mainland (Fig. 1). Indeed, the similarity of the forests in these two areas presumably contributed to the rush to add mammal species to the 'impoverished' forests of Newfoundland. Twelve species of mammals have been introduced, including moose (*Alces alces*), snowshoe hare (*Lepus americanus*) and red squirrels *Tamiasciurus hudsonicus* (Government of Newfoundland and Labrador 2007), while only 14 mammal species are considered native to Newfoundland (Dodds 1983). After a bit of natural-history-informed thought, it became evident that the key to the unique morphology of the Newfoundland crossbill was the absence of red squirrels on Newfoundland and their presence on the mainland (Benkman 1989; Parchman & Benkman 2002). Needless to say, the introduction of red squirrels was a bad omen for the Newfoundland crossbill. Red squirrels were introduced to Newfoundland in 1963 and the last Newfoundland crossbills may have been a pair on an islet off of Newfoundland

the year red squirrels colonized this islet in 1988. Thus, it took less than 30 years, for the introduction of a species initially present only 15 km away, to cause the decline and probable extinction of a species endemic to and apparently abundant on a rather large island (111 390 km²).

The occurrence of red squirrels is so important because they are both a strong selective agent on and pre-emptive competitor for the seeds in conifer cones (both red squirrels and crossbills are seed predators). The presence and absence of red squirrels and other tree squirrels (the other genus of tree squirrels is *Sciurus*) result in the evolution of quite different cone structures, which causes divergent selection on crossbills between areas with and without tree squirrels. Where tree squirrels are present, crossbills are less abundant as a result of competition for conifer seeds, selection by tree squirrels drives the evolution of seed defences and crossbills adapt to the average squirrel-defended cone. Where tree squirrels are absent, crossbills are much more abundant, and conifers lose squirrel defences and increase crossbill defences (Fig. 1). Crossbills evolve larger bills to adapt to these cones with increased crossbill defences (Fig. 1), and defences and counter-offences escalate in the absence of tree squirrels as a result of co-evolutionary arms races (Benkman 1999; Benkman *et al.* 2001, 2003; Parchman & Benkman 2002; Mezquida & Benkman 2005). The occurrence of local co-evolutionary arms races embedded in larger areas where tree squirrels are present causes divergent selection between populations of crossbills (i.e. a selection mosaic) that is strong enough to lead to high levels of reproductive isolation and to cause speciation (Smith & Benkman 2007).

Co-evolutionary arms races between crossbills and conifers have occurred on other oceanic islands such as Hispaniola (Parchman *et al.* 2007), but have also occurred on forested islands within continents. In isolated mountain ranges east and west of the Rocky Mountains where red squirrels are absent, crossbills have co-evolved with lodgepole pine (*Pinus contorta latifolia*) in a replicated manner (Benkman 1999; Benkman *et al.* 2001, 2003). As on Newfoundland, red squirrels were introduced into one of these mountain ranges east of the Rocky Mountains where an endemic crossbill evolved (the Cypress Hills: Benkman 1999; Benkman *et al.* 2001) but is now evidently extinct. The lodgepole pine forests in the Cypress Hills appear rather similar to the lodgepole pine forests in the Rocky Mountains (La Roi & Hnatiuk 1980), but not to a crossbill (or to a red squirrel!). Because lodgepole pine in the Cypress Hills, like black spruce (*Picea mariana*) on Newfoundland, had lost seed defences directed at red squirrels, the introduced red squirrels flourished at the expense of the endemic crossbills (Benkman 1993, 1999; Benkman *et al.* 2001). For example, the densities of red squirrels in the Cypress Hills are now upwards of four-times greater than in comparable habitat in other areas of the Rocky

Mountains (Benkman 1999). The evidence to date (Bruno *et al.* 2005) indicates that predator–prey interactions tend to be more co-evolved than other forms of interactions, thus we suspect that reductions in defences are more likely to contribute to the success of introductions than would evolutionary changes in response to the absence of competitors or mutualists.

Two characteristics of pine squirrels (*Tamiasciurus*) critical to such a selection mosaic are that they are very strong competitors for seeds in and selective agents on conifer cones (Benkman & Siepielski 2004) and they avoid crossing large (> 100 m) openings between forests. The limited dispersal of pine squirrels leads to areas with and without pine squirrels and a selection mosaic that leads to divergent evolutionary trajectories for crossbills in the different areas (Fig. 1). Thus, differences in community composition cause divergent selection and potentially speciation. Differences will be most pronounced where barriers to dispersal are greatest such as for nonvolant organisms on islands and freshwater aquatic species that also effectively occur on ‘islands’ within a sea of land. However, even for volant species on continents and marine species, there is often geographic variation in the community within which a given species interacts strongly (Strauss & Irwin 2004; Thompson 2005). Another example of such geographic variation in community composition contributing to variation in species interactions and evolution includes *Greya* moths that are pollinators and seed parasites of *Lithophragma* (Thompson & Cunningham 2002; Thompson & Fernandez 2006). Although well-characterized examples are few, we suspect that there will be an increasing number of such examples as researchers address the causes and evolutionary consequences of geographic variation in species interactions (Thompson 2005). We argue below that the presence and absence of strongly interacting species, particularly mammals, is especially likely to cause such selection mosaics, but first we discuss an emerging view of the geographic structure of species interactions. This enables us to provide a framework for discussing why local introductions should be successful and may involve serious consequences.

The geographic mosaic

Much of Earth’s biological diversity is a result of inter-specific interactions varying geographically among communities and ultimately causing populations within these different communities to evolve and co-evolve along unique pathways. The above example with crossbill populations co-evolving (Benkman *et al.* 2001, 2003; Parchman & Benkman 2002) and speciating (Smith & Benkman 2007) only in geographic areas without red squirrels provides a clear example of how this may occur. Here, we briefly review how an emerging view of the geographic structure

of species interactions, the geographic mosaic theory of co-evolution (Thompson 2005), pertains to local species introductions. Callaway *et al.* (2005) examined how this framework is useful for understanding plant introductions in relation to interactions in their rhizosphere, and have noted that the geographic mosaic of co-evolution may apply generally to species introductions and invasive species. Although there are three main parts of this theory, we focus on the first two because they are the most relevant for our discussion.

The first part is that interspecific interactions vary among populations, leading to selection mosaics that produce different evolutionary outcomes in different populations. Although selection mosaics can stem from variation in abiotic conditions, one common cause of selection mosaics is spatial variation in communities of interacting species (Strauss & Irwin 2004; Thompson 2005). Because groups of interacting species rarely have completely coincident ranges, and the divergent forms and outcomes of natural selection caused by varying species interactions across geographic space has been increasingly documented, geographic selection mosaics are likely a pervasive feature of species interactions (Thompson 2005). The second part is that because the strength of interactions often varies, some areas are co-evolutionary hotspots (populations where reciprocal selection and adaptation occur) and some are coldspots (populations where reciprocal selection and adaptation do not occur) (Thompson 2005). The same features creating selection mosaics often influence the occurrence of hot and coldspots across geographic space. The most important prediction is that natural selection will rarely favour the same traits across all populations and that co-evolved traits will rarely be fixed at the species level.

What have studies on the geographic mosaic of co-evolution revealed about the potential consequences of local introductions? They indicate that the strength and outcome of many interspecific interactions, co-evolving or otherwise, depend on the presence or absence of other species that are often found in neighbouring communities. Consequently, introducing other species from local, nearby communities that use similar resources and thus interact on a common interface has the potential to impact the outcome of the original interaction. Although our focus here is largely on the evolutionary and ecological impacts of local introductions on pairwise interactions between species, the presence or absence of one other species may also have indirect effects mediating evolutionary and ecological processes for other species. For instance, the evolution of lodgepole pine seed defences in response to selection exerted by red squirrels also acts to suppress seed predation by another seed predator, the lodgepole pine cone borer moth (*Eucosma recissoriana*), because the evolved defences that deter red squirrels also deter moths. Conversely, the loss of seed defences in response to

relaxation of selection by red squirrels appears to allow greater seed predation by moths (Siepielski & Benkman 2004). While other types of introductions (i.e. transcontinental, etc.) can just as easily cause these potential effects, local introductions may seem less innocuous simply because the introduced species may occur in other local communities. In light of this framework, we now consider the evidence for why an introduction into areas near a species' home location is likely to succeed more often than if introduced farther away.

Local introductions are more successful

Abiotic conditions

Minimally, invaders require environmental conditions they can tolerate to be successful. One pathway therefore is for the species' tolerances to match the conditions of the invaded habitat (Peterson 2003). One of the best predictors of successful invasion by fishes in California is a match between the invaded habitat and the habitat of origin (Moyle & Marchetti 2006). Likewise, successful introductions of rainbow trout (*Oncorhynchus mykiss*) are limited to situations where their life history is compatible with the hydrological regime (Fausch *et al.* 2001) and the spread of Argentine ants (*Linepithema humile*) is limited by unfavourable abiotic conditions (Holway *et al.* 2002b). Several studies on birds and mammals also reveal that the suitability of the abiotic environment (as measured by the match between the latitudes or climate of origin and site of introduction, i.e. 'climate matching') is critical for the success of species introductions (Blackburn & Duncan 2001; Duncan *et al.* 2001). An alternative pathway to success is to have wide physiological tolerances. For example, fishes with wide physiological tolerances are more likely to invade watersheds in California (Marchetti *et al.* 2004) and bird species occupying larger geographic areas, and presumably having wider physiological tolerances, are more likely to persist after being introduced (Blackburn & Duncan 2001).

If abiotic similarity or compatibility is important, then species should often be able to invade nearby areas more readily than more distant areas. Such a pattern was found for fish invasions in California (Marchetti *et al.* 2004). Similarly, analyses of translocations of birds and mammals show that they are more likely to persist when moved into the core than into the periphery or outside of the species' historic geographic range (Wolf *et al.* 1998). On a coarser scale, birds were more likely to succeed if introduced into the biogeographic region of origin than if introduced into a new biogeographic region (Blackburn & Duncan 2001). This could also reflect the ease at which more similar biotic communities can be invaded. Not only are nearby areas likely to have suitable abiotic conditions, but they also

harbour populations of suitable prey and other species (potential predators, competitors) with which a given species has evolved. Importantly, the prey of the potential invader may have lost or never evolved defences facilitating invasion.

Biotic changes in the absence of species

Species evolving in the absence of enemies are expected to lose defences that are costly to produce or maintain. The more generations a species evolves in the absence of their enemies and the more costly the defences, the more likely the defences will be lost. Several studies have shown that species that have evolved in the absence of predators or other enemies for thousands of years have lost defences that their ancestors had presumably evolved in the presence of enemies (e.g. Bowen & Van Vuren 1997). Other studies have shown that different predators favour the evolution of different sets of defences in different prey species, with variation in predator composition presumably causing divergent selection between ancestral prey populations contributing to their diversification (McPeck *et al.* 1996). Few studies however, have quantified the loss of defences between populations of a single species. One such study was by Zangerl & Berenbaum (2005). They found that less than 300 years after being introduced into North America, wild parsnip (*Pastinaca sativa*) apparently evolved lower concentrations of toxic furanocoumarins in the absence of its main herbivore, the parsnip webworm (*Depressaria pastinacella*). Wild parsnip then rapidly re-evolved higher concentrations within 100 years after the webworm was accidentally introduced. Similarly, the red cedar *Thuja plicata* that have colonized the Queen Charlotte Islands, and evolved in the absence of ungulate herbivores during the past 10 000 years, have less chemical defence and are preferred by black-tailed deer (*Odocoileus hemionus*) over red cedar from the mainland where deer are present (Vourc'h *et al.* 2001). This decrease in plant defences presumably explains why the recently introduced deer on the Queen Charlotte Islands are depleting red cedar (and other plants) to such a great extent (Vourc'h *et al.* 2001). Perhaps for the same reason (predators of the deer are also absent), the introduced deer, much like introduced red squirrels on Newfoundland and in the Cypress Hills, now occur at densities higher than their mainland counterparts. The reduction in defences presumably enables introduced consumers to persist and rapidly increase in population size following their introduction. The combination of suitable abiotic conditions and fewer defences by potential victims should lead to particularly high success rates for local introductions. For example, 11 out of 12 introductions of mammals onto Newfoundland succeeded (Government of Newfoundland & Labrador 2007). This is a much higher success rate than the usual one in 10 or 'tens rule'

(Williamson & Fitter 1996). Nine of the 11 species successfully introduced onto Newfoundland are found on the adjacent mainland, and two others are the widespread and invasive Norwegian rat (*Rattus norvegicus*) and house mouse (*Mus musculus*). The one unsuccessful introduction was of bison (*Bison bison*), for which the nearest population is over 2900 km to the west. High success rates of introductions have also been found for mammals being introduced onto other islands (e.g. nearly 60% in New Zealand where there are no native land mammals; Courchamp *et al.* 2003), as well as between continents (Jeschke & Strayer 2005).

Some effects of local introductions

Although we do not expect that local introductions of species will be of greater conservation concern than more distant introductions, we suspect that the adverse effects are likely to go unnoticed (although this is true for most introductions; Simberloff 1991). Indeed, the few studies concerning local introductions that we have found are a testament to this. Because local introductions will act to homogenize communities, it is difficult to detect their effects without baseline studies prior to the introduction. For example, prior to our research no one in either Newfoundland or the Cypress Hills (a provincial park) even suspected that the endemic crossbills there were declining or threatened, let alone extinct. By homogenizing nearby communities, local introductions reduce the geographic diversity of interactions a species experiences. This eliminates an important source of geographically variable and divergent selection between populations, which results in a reduction in genetic and phenotypic variation that may be critical to persistence and adaptation to a changing environment. For example, the occurrence of gene flow across geographic selection mosaics increases the likelihood that polymorphisms are maintained in local interactions, and may contribute to the persistence of local interactions and the long-term maintenance of genetic variation within species (Gomulkiewicz *et al.* 2000; Thompson 2005). In addition, the erosion of geographic selection mosaics may eliminate perhaps the most important engine of speciation — geographically divergent selection among populations (Schluter 2000; Funk *et al.* 2006).

Strongly interacting species: their importance can be a curse

Strongly interacting species are often considered as those species that have the ability to alter system structure (Paine 1980). Although most discussion of strongly interacting species pertains to ecological interactions (e.g. keystone species), we have found that such species can also have very pronounced evolutionary effects on other species (Benkman & Siepielski 2004). For example, in the absence

of a strongly interacting species, potential prey are likely to rapidly lose defences directed at them; more so than in the absence of a weakly interacting species. Other species such as competitors are also more likely to respond evolutionarily because of evolutionary changes in their formerly shared prey and the absence of a competitor, and be even more susceptible to the introduction of the strongly interacting species.

Particularly dramatic examples of the adverse effects of introducing strongly interacting species include introduced predatory mammals causing numerous bird extinctions on oceanic islands (Courchamp *et al.* 2003; Blackburn *et al.* 2004), but also cases that qualify as more local introductions such as the introduction of fishes into fishless alpine lakes in the Sierra Nevada, California that have caused severe reductions or local extinctions of frogs *Rana muscosa*, some benthic macroinvertebrates and large zooplankton (Knapp *et al.* 2001). Strongly interacting species are also known for their indirect effects that cascade through the community (i.e. keystone species; Paine 1966; Carpenter *et al.* 1985; Estes & Duggins 1995).

Indeed, because of these strong effects, especially of top predators, some have argued for the importance of protecting large mammals that act as keystone predators in communities (Terborgh *et al.* 1999). However, other mammals beside predators also have strong direct and indirect effects especially on land. We have already mentioned some effects of the granivorous red squirrel, and later we will discuss some of their other important direct and indirect effects. Kangaroo rats (*Dipodomys* spp.) are granivores in the deserts of North America that alter plant assemblages by differentially preying upon large-sized seeds, and one species of kangaroo rat (*D. spectabilis*) builds large burrow mounds that further alter community composition and ecosystem processes (Brown 1998). Small granivorous mammals are also known to affect plant assemblages in temperate deciduous forests (e.g. Ostfeld *et al.* 1997). A number of studies indicate that herbivorous mammals have a considerable impact on the composition of plant assemblages (Owen-Smith 1987; Paine 2000; Howe *et al.* 2006). For example, large ungulate herbivores have major direct effects on plant assemblages, which have substantial indirect effects on the animal communities as well (Côté *et al.* 2004; Ripple & Beschta 2006b; Pringle *et al.* 2007). Although there is some disagreement as to the relative importance of insect and vertebrate herbivory on plant population dynamics (Crawley 1989; Bigger & Marvier 1998), mammalian herbivory, unlike insect herbivory, commonly alters floristic composition (Crawley 1989; Paine 2000). In further support of the strong impacts of mammalian herbivores, the presence of native vertebrate (nearly exclusively mammals) herbivores much more than invertebrate herbivores limits the success of introduced plants (Parker *et al.* 2006). Consequently, we agree with Terborgh and

others (Terborgh *et al.* 1999; Soulé *et al.* 2003) that keeping strongly interacting species in the community should be a conservation priority and when they have recently been extirpated that re-introducing them is potentially a valuable conservation strategy.

However, the strong impacts that are so crucial for shaping the structure of communities can lead to rather adverse consequences from the introduction of strongly interacting species when the communities have evolved in their absence even for a relatively brief time such as the past 9000 years (e.g. red squirrels introduced onto Newfoundland). The numerous examples of rapid evolution (Thompson 1998) and geographic selection mosaics (Thompson 2005) further this concern. Thus, we do not agree that introducing strongly interacting species (or surrogates for them) after they have been absent for thousands of years, which is sufficient for considerable evolutionary responses, is a worthwhile conservation strategy (*contra* Donlan *et al.* 2006). This is unlike and should not be equated to the benefits of, for example, re-introducing gray wolves (*Canis lupus*) to Yellowstone National Park 70 years after they were extirpated (Ripple & Beschta 2006a).

Strongly interacting species: the age of mammals

If avoiding the introduction of strongly interacting species is a good conservation strategy (as is avoiding their extinction in native habitats), it would be helpful if we could anticipate which species are likely to be strongly interacting. In aquatic systems, fish often have keystone effects (Carpenter *et al.* 1985) and when introduced have caused numerous extinctions (Witte *et al.* 1992; Knapp *et al.* 2001). On land, ants have diverse and important effects on communities (Hölldobler & Wilson 1990; pp. 1–2), with the introduction of certain ant species (e.g. Argentine ant) causing declines of other species with adverse effects on seed dispersal and plant communities (Christian 2001; see Holway *et al.* 2002a for a review on ant introductions).

Here we would like to emphasize mammals. Mammals, especially as top predators, have strong effects on communities on both land and in water (Estes 1996; Terborgh *et al.* 2001; Springer *et al.* 2003; Johnson *et al.* 2006), and their introductions have often led to extinctions (Courchamp *et al.* 2003; Cox & Lima 2006) and massive impacts on ecosystems (Courchamp *et al.* 2003; Croll *et al.* 2005). An indication of the ecological importance of mammals (in terms of their energy transfer/consumption) and the potential strength of their species interactions is their relatively high population densities compared to birds, which are the other taxon with high mass-specific energy demands. Mammals tend to occur at population densities and consume energy at rates that are at least an order of magnitude greater than that of birds for any given body mass and there are no extant birds comparable to the larger

Table 1 The percentage of 1559 introductions of 330 species of birds and mammals causing a negative impact from herbivory (including habitat changes) and predation (data from Ebenhard 1988)

Introduced taxa	Herbivory	Predation	Total effects
Birds	0.4	1.4	1.8
Mammals	20.0	17.0	37.0

Table 2 The frequency of serotiny and postfire seedling densities for Rocky Mountain lodgepole pine (*Pinus contorta latifolia*) in (A) an isolated mountain range without red squirrels *Tamiasciurus hudsonicus* (serotiny data from Benkman & Siepielski 2004; seedling density data from Newsome & Dix 1968 measured prior to the introduction of red squirrels in 1950) and (B) in three areas within Yellowstone National Park where red squirrels are present (data from Turner *et al.* 2003)

Location	Pre-fire stand serotiny (percentage of lodgepole pine)	Post-fire lodgepole pine seedling density (stems/ha)
A.		
Cypress Hills	92	2 500 000
B.		
Cougar Creek	65	211 000
Fern Cascades	10	2 300
Yellowstone Lake	< 1	600

mammals (Silva *et al.* 1997). A much stronger ecological (conservation) impact of mammals relative to birds is supported by data on their introductions. The frequencies at which impacts are detected on other species from herbivory and predation are over an order of magnitude greater for introduced mammals than for introduced birds (Table 1). Moreover, the impact of introduced mammalian herbivores on native plants is greater than that of introduced invertebrates (Crawley 1989; see also Ebenhard 1988). A stronger ecological impact would presumably result in a greater evolutionary impact on other species (e.g. Steinberg *et al.* 1995; see also Callaway *et al.* 2005). We return to the diverse impacts of red squirrels as a clear example.

Geographic variation in the presence of red squirrels has diverse effects in lodgepole pine forest ecosystems, which dominate some 20 million ha in North America. First, selection by red squirrels leads to a reduction in the frequency of serotiny in lodgepole pine (the retention of seeds in cones until they are heated such as by a fire; Benkman & Siepielski 2004). Because the frequency of serotiny influences the density of pine seedlings after a fire (Table 2), which in turn affects subsequent plant and animal communities, and biogeochemical processes (Tinker *et al.* 1994; Turner *et al.* 2003), red squirrels act as 'keystone

selective agents' (Benkman & Siepielski 2004). Squirrels also remove a large fraction of the cones, so that after a fire the densities of seedlings are up to 2.5 million per hectare in the absence of squirrels (Table 2) compared to only 3–4 and up to 211 000 seedlings per hectare in areas having squirrels (Table 2; Tinker *et al.* 1994; Turner *et al.* 2003). In the Cypress Hills, the introduction of red squirrels has caused a decrease in the canopy seed bank (Benkman 1999) so that following the next stand-replacing fire the density of seedlings will be reduced considerably. In time, selection by red squirrels will presumably cause the frequency of serotiny and thus the density of seedlings following fires to further decrease with concomitant effects on succession and ecosystem processes. Second, as mentioned earlier, the introduction of red squirrels into the Cypress Hills has led to the extinction of a distinct crossbill that owed its existence to the absence of red squirrels. Third, the introduction of red squirrels into the Cypress Hills has apparently caused a reduction in the abundances of breeding birds that nest in sites susceptible to predation by red squirrels (Siepielski 2006). In short, the local introduction of one strongly interacting species has tremendous ecological and evolutionary consequences, many of which would go unnoticed without careful study.

Fortunately, most introductions of mammals have been deliberate (Courchamp *et al.* 2003), thus with care we should be able to reduce if not eliminate them (see Jeschke & Strayer 2005 for cessation of intercontinental introductions). However, local and intentional introductions of large mammals continue. For example, the Colorado Division of Wildlife is currently (2006–2007) introducing moose into areas (e.g. Grand Mesa, Colorado) south of their native distribution. This is occurring in spite of studies to the north (Wyoming) showing that moose occurring in areas where predators had been largely extirpated (their potential predators have also been extirpated from Colorado), over-browse willows (*Salix* spp.) and thereby causes a considerable reduction in migratory songbird populations (Berger *et al.* 2001). This appears to be a representative and, unfortunately, an all too frequent example of how mammals are still being introduced (e.g. Cox *et al.* 1997).

Conclusions

Local introductions should often be successful because abiotic conditions are likely to be suitable and potential prey species may have lost defences. The longer the time the community has evolved in the absence of the introduced species and the stronger it interacts with other species, the more likely the introduced species will have pronounced consequences on other species and even ecosystem processes. Mammals in particular, and especially those with limited dispersal abilities, should not

be introduced because they generally have considerable ecological and likely evolutionary impacts. Although an important conservation strategy is to re-introduce strongly interacting species if they have been extirpated recently, it is unwise to introduce them (i.e. the rewilding idea of Donlan *et al.* 2006) if they have been absent for time periods sufficient for considerable evolutionary change (e.g. often only a few thousand years). The remaining community members will likely have evolved considerably in the absence of the strongly interacting species, which facilitates its introduction but more importantly increases the vulnerability of the existing community members.

Acknowledgements

National Science Foundation grants (DEB-0455705 and DEB-0515735) to C.W.B. and an Environmental Protection Agency GRO Fellowship to T.L.P. provided financial support during the writing of this manuscript.

References

- Benkman CW (1989) On the evolution and ecology of island populations of crossbills. *Evolution*, **43**, 1324–1330.
- Benkman CW (1993) Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. *Ecological Monographs*, **63**, 305–325.
- Benkman CW (1999) The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *American Naturalist*, **154**, S75–S91.
- Benkman CW, Holimon WC, Smith JW (2001) The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. *Evolution*, **55**, 282–294.
- Benkman CW, Parchman TL, Favis A, Siepielski AM (2003) Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. *American Naturalist*, **162**, 182–194.
- Benkman CW, Siepielski AM (2004) A keystone selective agent? Pine squirrels and the frequency of serotiny in lodgepole pine. *Ecology*, **85**, 2082–2087.
- Berger J, Stacey PB, Bellis L, Johnson MP (2001) A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian Neotropical migrants. *Ecological Applications*, **11**, 947–960.
- Bigger DS, Marvier M (1998) How different would a world without herbivory be? A search for generality in ecology. *Integrative Biology*, **1**, 60–67.
- Blackburn TM, Duncan RP (2001) Determinants of establishment success in introduced birds. *Nature*, **414**, 195–197.
- Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. *Science*, **305**, 1955–1958.
- Bowen L, Van Vuren D (1997) Insular endemic plants lack defences against herbivores. *Conservation Biology*, **11**, 1249–1254.
- Brown JH (1998) The desert granivory experiments at Portal. In: *Issues and Perspectives in Experimental Ecology* (eds Reseraris WL, Bernardo J), pp. 71–95. Oxford University Press, New York.
- Bruno JF, Fridley JD, Bromberg KD, Bertness MD (2005) Insights into biotic interactions from studies of species invasions. In: *Species Invasions: Insights Into Ecology, Evolution, and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 13–40. Sinauer & Associates, Sunderland, Massachusetts.
- Callaway RM, Hierro JL, Thorpe AS (2005) Evolutionary trajectories in plant and soil microbial communities: *Centaurea* invasions and the geographic mosaic of coevolution. In: *Species Invasions: Insights Into Ecology, Evolution, and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 341–363. Sinauer & Associates, Sunderland, Massachusetts.
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *Bioscience*, **35**, 634–639.
- Christian CE (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature*, **413**, 635–639.
- Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 113–147.
- Courchamp F, Chapuis J, Pascal M (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, **78**, 347–383.
- Cox JA, Quinn TG, Boyter HH Jr. (1997) Management by Florida's game and fresh water fish commission. In: *Strangers in paradise: impact and management of nonindigenous species in Florida* (eds Simberloff D, Schmitz DC, Brown TC), pp. 297–316. Island Press, Covelo, California.
- Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution*, **21**, 674–680.
- Crawley MJ (1989) The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. In: *Insect-Plant Interactions* (ed. Bernays EA), pp. 45–71. CRC Press, Boca Raton, Florida.
- Croll DA, Maron JL, Estes JA, Danner EM, Byrd GV (2005) Introduced predators transform subarctic islands from grassland to tundra. *Science*, **307**, 1959–1961.
- Dodds DG (1983) Terrestrial mammals. In: *Biogeography and Ecology of the Island of Newfoundland* (ed. Robin South G), pp. 509–550. Dr. W. Junk Publishers, The Hague. The Netherlands.
- Donlan DJ, Berger J, Bock CE *et al.* (2006) Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. *American Naturalist*, **168**, 660–681.
- Duncan RP, Bomford M, Forsyth DM, Conibear L (2001) High predictability in introduction outcomes and geographic range size of introduced Australian birds: a role for climate. *Journal of Animal Ecology*, **70**, 621–632.
- Ebenhard T (1988) Introduced birds and mammals and their ecological effects. *Swedish Wildlife Research*, **13**, 1–107.
- Estes JA (1996) Predators and ecosystem management. *Wildlife Society Bulletin*, **24**, 390–396.
- Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs*, **65**, 75–100.
- Fausch KD, Taniguchi Y, Nakano S, Grossman GD, Townsend CR (2001) Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. *Ecological Applications*, **11**, 1438–1455.
- Funk DJ, Nosil P, Etges WJ (2006) Ecological divergence exhibits consistently positive associations with reproductive isolation across disparate taxa. *Proceedings of the National Academy of Sciences, USA*, **103**, 3209–3213.
- Gomulkiewicz R, Thompson JN, Holt RD, Nuismer SL, Hochberg ME (2000) Hot spots, cold spots, and the geographic mosaic theory of coevolution. *American Naturalist*, **156**, 156–174.

- Government of Newfoundland and Labrador (2007) <http://www.env.gov.nl.ca/snp/Education/LandMammals.htm> (accessed 15 January 2007).
- Hölldobler B, Wilson EO (1990) *The Ants*. Belknap Press, Cambridge, Massachusetts.
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002a) The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, **33**, 181–233.
- Holway DA, Suarez AV, Case TJ (2002b) Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. *Ecology*, **83**, 1610–1619.
- Howe HF, Zorn-Arnold B, Sullivan A, Brown J (2006) Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology*, **87**, 3007–3013.
- Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences, USA*, **102**, 7198–7202.
- Johnson CN, Isaac JL, Fisher DO (2006) Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **274**, 341–346.
- Knapp RA, Matthews KR, Sarnelle O (2001) Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs*, **71**, 401–421.
- La Roi GH, Hnatiuk RJ (1980) The *Pinus contorta* forests of Banff National Park and Jasper National Park: a study in comparative synecology and syntaxonomy. *Ecological Monographs*, **50**, 1–29.
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Marchetti MP, Moyle PB, Levine R (2004) Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications*, **14**, 587–596.
- Mayr E (1963) *Animal Species and Evolution*. Belknap Press, Cambridge, Massachusetts.
- McPeck MA, Schrot AK, Brown JM (1996) Adaptation to predators in a new community: swimming performance and predator avoidance in damselflies. *Ecology*, **77**, 617–629.
- Mezquida ET, Benkman CW (2005) The geographic selection mosaic for squirrels, crossbills, and Aleppo pine. *Journal of Evolutionary Biology*, **18**, 348–357.
- Moyle PB, Marchetti MP (2006) Predicting invasion success: freshwater fishes in California as a model. *BioScience*, **56**, 515–524.
- Newsome RD, Dix RL (1968) The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. *American Midland Naturalist*, **80**, 118–185.
- Ostfeld RS, Manson RH, Canham CD (1997) Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology*, **78**, 1531–1542.
- Owen-Smith N (1987) Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology*, **13**, 351–362.
- Paine RT (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.
- Paine RT (1980) Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, **49**, 667–685.
- Paine RT (2000) Phycology for the mammalogist: marine rocky shores and mammal-dominated communities—how different are the structuring processes? *Journal of Mammalogy*, **81**, 637–648.
- Parchman TL, Benkman CW (2002) Diversifying coevolution between crossbills and black spruce on Newfoundland. *Evolution*, **56**, 1663–1672.
- Parchman TL, Benkman CW, Mezquida ET (2007) Coevolution between Hispaniolan crossbills and pine: Does more time allow for greater phenotypic escalation at lower latitude? *Evolution*, in press.
- Parker JD, Burkepile DE, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459–1461.
- Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology*, **78**, 419–433.
- Pringle RM, Young TP, Rubenstein DI, McCauley DJ (2007) Herbivore-initiated cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences, USA*, **104**, 193–197.
- Ripple WJ, Beschta RL (2006a) Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management*, **230**, 96–106.
- Ripple WJ, Beschta RL (2006b) Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation*, **133**, 397–408.
- Schluter D (2000) *The Ecology of Adaptive Radiations*. Oxford University Press, New York.
- Siepielski AM (2006) A possible role for red squirrels in structuring breeding bird communities in lodgepole pine forests. *Condor*, **108**, 232–238.
- Siepielski AM, Benkman CW (2004) Interactions among moths, crossbills, squirrels and lodgepole pine in a geographic selection mosaic. *Evolution*, **58**, 95–101.
- Silva M, Brown JH, Downing JA (1997) Differences in population density and energy use between birds and mammals: a macroecological perspective. *Journal of Animal Ecology*, **66**, 327–340.
- Simberloff DS (1991) Keystone species and community effects of biological introductions. In: *Assessing Ecological Risks of Biotechnology* (ed. Ginzburg LR), pp. 1–19. Butterworth-Heinemann, Boston, Massachusetts.
- Smith JW, Benkman CW (2007) A coevolutionary arms race causes ecological speciation in crossbills. *American Naturalist*, **169**, 455–465.
- Soulé ME, Estes JA, Berger J, Martinez del Rio C (2003) Ecological effectiveness: conservation goals for interactive species. *Conservation Biology*, **17**, 1238–1250.
- Springer AM, Estes JA, van Vliet GB *et al.* (2003) Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences, USA*, **100**, 12223–12228.
- Steinberg PD, Estes JA, Winter FC (1995) Evolutionary consequences of food chain length in kelp forest communities. *Proceedings of the National Academy of Sciences, USA*, **92**, 8145–8148.
- Strauss SY, Irwin RE (2004) Ecological and evolutionary consequences of multispecies plant–animal interactions. *Annual Review of Ecology and Systematics*, **35**, 435–466.
- Terborgh J, Estes JA, Paquet P *et al.* (1999) The role of top carnivores in regulating terrestrial ecosystems. In: *Continental Conservation: Scientific Foundations of Regional Reserve Networks* (eds Soulé M, Terborgh J), pp. 39–54. Island Press, Washington, D.C.
- Terborgh J, Lopez L, Nuñez VP *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1926.
- Thompson JN (1998) Rapid evolution as an ecological process. *Trends in Ecology & Evolution*, **13**, 329–332.
- Thompson JN (2005) *The Geographic Mosaic of Coevolution*. University Chicago Press, Chicago, Illinois.

- Thompson JN, Cunningham BM (2002) Geographic structure and dynamics of coevolutionary selection. *Nature*, **417**, 735–738.
- Thompson JN, Fernandez CC (2006) Temporal dynamics of antagonism and mutualism in a geographically variable plant–insect interaction. *Ecology*, **87**, 103–112.
- Tinker DB, Romme WH, Hargrove WW, Gardner RH, Turner MG (1994) Landscale-scape heterogeneity in lodgepole pine serotiny. *Canadian Journal of Forest Research*, **24**, 897–903.
- Turner MG, Romme WH, Tinker DB (2003) Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, **1**, 351–358.
- Vourc'h G, Martin J, Duncan P, Escarré J, Clausen TP (2001) Defensive adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and island populations. *Oecologia*, **126**, 84–93.
- Williamson M, Fitter A (1996) The varying success of invaders. *Ecology*, **77**, 1661–1666.
- Witte F, Goldschmidt T, Wanink J *et al.* (1992) The destruction of an endemic species flock: quantitative data on the decline of haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes*, **34**, 1–28.
- Wolf CM, Garland T Jr, Griffith B (1998) Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biological Conservation*, **86**, 243–255.
- Zangerl AR, Berenbaum MR (2005) Increase in toxicity of an invasive weed after reassociation with its coevolved herbivore. *Proceedings of the National Academy of Sciences, USA*, **102**, 15529–15532.

Craig Benkman is an evolutionary ecologist and professor at the University of Wyoming who is increasingly using his research to address conservation-related issues. Both Adam Siepielski and Thomas Parchman are graduate students finishing their dissertations in Benkman's lab. Adam is interested in how community context influences micro- and macroevolutionary processes, particularly those related to coevolution. Tom's research involves the interface between ecology, evolution, and genetics with a focus on coevolution and adaptive radiations.
