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Biological Invasions on Oceanic Islands: Implications for Island Ecosystems and Avifauna

해양 도서에서의 생물 침입: 도서 생태계와 도서 조류상에 대한 의미

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Abstract

Biological invasions present a global threat to biodiversity, but oceanic islands are the systems hardest hit by invasions. Islands are generally depauperate in species richness, trophic complexity, and functional diversity relative to comparable mainland ecosystems. This situation results in low biotic resistance to invasion and many empty niches for invaders to exploit. It also results in island species being poorly adapted for dealing with predators, herbivores, and strong competitors. Hence, invaders tend to be more successful on oceanic islands and their impacts tend to be much stronger, often resulting in species extinctions and restructuring of communities and ecosystem functions. Birds play particularly important ecological roles on oceanic islands, where they are generally the most diverse terrestrial vertebrate group due to the general absence of mammals and low diversity of reptiles and amphibians. As a result, birds can completely dominate or contribute very strongly to various key functional roles such as herbivory, pollination, seed dispersal, predation, ecosystem engineering, and nutrient transport. For similar reasons, island birds are very susceptible to invader impacts and are important system-level transmitters of invader impacts. Invasive species management on islands is challenging, but some of the same factors that render islands particularly sensitive to biological invasions also favor successful invasive species management. The small size and isolation of many islands ensures relatively small invader

populations and discrete management areas that facilitate extirpation of the invader and its exclusion following eradication. In recent decades, island invasives management has focused on extirpation of exotic species and hundreds of islands have been cleared of exotic predators, herbivores, and sometimes plants. In most situations, invader extirpation has helped to restore the system, but in numerous cases restoration has failed due to complex side effects. Taking a broader community-level approach to invasive species management on islands will help improve success and reduce unexpected deleterious side effects.

요 약

생물 침입은 생물다양성 전반에 걸쳐 위협적인 현상이지만, 특히 해양 도서들은 생물 침입에 가장 큰 타격을 받은 생태계에 해당된다. 일반적으로 섬은 유사한 육상 생태계에 비해 종 풍부도, 영양단계의 복잡성, 기능적 다양성 등이 상대적으로 빈약하다. 이로 인해 외래종의 침입에 대한 생물 저항성이 낮으며, 침입종이 이용할 수 있는 생태적 지위가 많이 비어있게 된다. 또 이런 특징들은 섬에 서식하는 생물종이 포식자, 초식동물, 강력한 경쟁종들에 대처하는 적응력이 빈약한 결과로 연결된다. 따라서 침입종은 해양 도서에서 더욱 성공적으로 정착하고 그 영향은 더욱 강하게 나타나는 경향이 있으며, 이로 인해 멸종을 비롯하여 생물 군집과 생태계 기능의 재구성되는 결과도 종종 나타난다. 해양 도서에는 종종 포유류가 없고 파충류와 양서류의 다양성이 낮은 환경이 조성되므로, 조류는 섬에서 가장 다양한 육상 척추동물군으로서 특별히 중요한 생태적 역할을 담당한다. 결과적으로 조류는 섭식, 수분, 종자 산포, 포식, 생태계 조정, 영양분 이동 등 다양하고 핵심적인 기능을 담당하는 완벽한 우점 또는 매우 강력한 기여자 역할을 할 수 있다. 비슷한 이유에서 섬의 조류들은 침입자의 영향에 매우 민감할 뿐만 아니라, 침입자의 영향을 생태계 수준에서 전달하는 중요한 분류군에 해당한다. 섬에서의 침입종 관리는 쉽지 않은 과제이지만, 섬 생태계가 생물 침입에 특히 민감하게 만드는 요인 중 일부는 오히려 성공적인 침입종 관리에 도움이 될 수도 있다. 많은 섬들은 면적이 좁고 고립된 환경을 유지하므로, 침입종의 개체군이 상대적으로 작고 관리지역이 각각 구분되어 있어서 침입종을 손쉽게 제거할 수 있고 구제 작업 이후에는 침입종이 없는 상태를 유지하기에도 유리하다. 최근 수십 년간 도서 지역의 침입종 관리는 외래종의 구제에 초점을 두어 왔으며, 수백여 개의 섬에서 외래 포식자와 초식동물, 일부 식물이 성공적으로 제거되었다. 대부분의 경우 침입종 제거는 생태계 복원에 도움이 되어 왔으나, 복잡한 부작용으로 인해 많은 복원 사례가 실패하기도 하였다. 따라서 도서 지역의 침입종 관리에 있어서 성공률을 높이고 예상치 못한 유해한 부작용을 줄이기 위해서는 더욱 폭넓은 군집 수준의 접근 방식을 취하는 것이 도움이 될 것이다.

Introduction

Biological invasions are considered the second greatest threat to global biodiversity following habitat destruction (Wilcove et al. 1998), but present an even greater threat to fragile oceanic island ecosystems (Brockie et al. 1988, Tershy et al. 2002). Although island ecosystems are generally more buffered against anthropogenic habitat destruction than mainland systems, they are highly susceptible to biological invasions and inherently sensitive to invader impacts (Elton 1958, Diamond 1989, Clavero et al. 2009). Islands are generally depauperate in species richness, trophic complexity, and functional diversity relative to comparable mainland ecosystems (Vitousek 1990). This results in little biotic resistance to invaders and a high availability of empty niches. For example, plant diversity on oceanic islands is generally low, terrestrial herbivores are usually rare and carnivores are commonly absent (Carlquist 1974, Pimm 1991, Denslow 2003). This means that invasive plants and herbivores may encounter little competition from natives and little consumer pressure, and invasive predators commonly discover an undisputed buffet. Island invaders may similarly find themselves released from formerly repressive diseases (Dobson 1988). As a result, biological invaders are more successful at establishing and proliferating on islands than on mainland systems (e.g., Vitousek et al. 1997). In fact, commensal species like Norway rats (*Rattus norvegicus*) and house mice (*Mus musculus*), which tend to be restricted to peridomestic habitats in diverse continental systems like North America (Foresman 2001), thrive across a range of natural habitats on islands (Jones et al. 2007), presumably due in part to release from competition and predation.

Invader impacts are also generally stronger on oceanic islands, commonly resulting in extinction. Most extinctions of amphibians and reptiles (82%), bird species or subspecies (94%), and mammals (67%) recorded in recent times, have occurred on islands (Ricketts et al. 2005). The majority of these extinctions as well as threats to currently imperiled species have been attributed to exotic species invasions (e.g., King 1985, Courchamp et al. 2003, Blackburn et al. 2004). This is because the low species and functional diversity inherent in island biota leave island residents poorly adapted to defend against invader impacts. For example, due to the lack of substantive herbivore pressure or, in some cases, the absence of herbivores, many island plant species have not evolved life history strategies or physical and chemical traits that protect them against herbivores (e.g., Bowen and Van Vuren 1997). Likewise, many island vertebrates have not developed life history strategies and physical and behavioral traits that protect them against predators (Stone et al. 1994, Courchamp et al. 2003). Flightless birds such as moas (Dinornithidae) provide a classic example of this, but recent studies indicate some island birds may develop behavioral anti-predator adaptations in response to exotic predators (Massaro et al. 2008). Although less well recognized, community-level manifestations of such vulnerabilities also exist. For instance, in the absence of erect woody vegetation, birds and other vertebrates are forced to nest on the ground where they are more vulnerable to exotic predators. Oceanic islands are also more sensitive to invader impacts at the ecosystem level. Island ecosystems are commonly dependent upon allochthonous (out-of-system) nutrient inputs brought inland from seabirds and other animals (e.g., Polis and Hurd 1996, Sanchez-Pinero and Polis 2000). Additionally, vegetation plays important roles in buffering some island systems from violent storms and mitigating erosion from high rainfall. Thus, exotic species that suppress or extirpate functionally integral native plant and animal species can alter entire ecosystem dynamics on oceanic islands (e.g., O'Dowd et al. 2003, Croll et al. 2005, Fukami et al. 2006). In general, due to the low diversity of island systems, a high proportion of individual species may play critical functional roles and lack functional equivalents to replace them when suppressed or extirpated - hence loss of the species results in loss of ecosystem function.

Avian ecology and oceanic islands

Birds play integral and often unique roles in ecosystems. As a highly diverse and extremely vagile vertebrate group, they serve as important nutrient transporters, spore dispersers, pollinators, herbivores, insectivores, scavengers, predators, and ecosystem engineers (Sekercioglu et al. 2004, Sekercioglu 2006). Birds are particularly ecologically important groups on oceanic islands, where they are generally the most diverse terrestrial vertebrate taxa due to the general absence of mammals and low diversity of reptiles and amphibians. As a result, they can completely dominate or contribute very strongly to various key functional roles such as herbivory, pollination, seed dispersal, predation, ecosystem engineering, and nutrient transport (Clout and Hay 1989, Furness 1991, Sanchez-Pinero and Polis 2000, Sekercioglu 2006). In intertidal systems, birds can determine community structure and serve as keystone predators (Wootton 1994, Kurle et al. 2008). For example, Kurle et al. (2008) showed on the Aleutian Islands that feeding by certain seabirds within the intertidal zone created a kelp-dominated system by controlling herbivores. However, when introduced rats were present, they suppressed the birds and released the herbivores which consumed the kelp and shifted the system to one dominated by sessile invertebrates. Inland, the allochthonous nutrients carried by seafaring birds in the form of guano can define terrestrial plant communities (Sanchez-Pinero and Polis 2000, Croll et al. 2005). In addition, birds may play important roles in determining island species composition as natural vectors for introductions of plants and some higher organisms (Magnusson and Magnussun 2000, Scott et al. 2001).

Invasive species on oceanic islands?

Exotic invaders represent a great variety of taxonomic forms and ecological strategies. They can be microorganisms, invertebrates, plants, amphibians, reptiles, birds, or mammals.

2009). Thus, in discussing invasive species management on islands, it is important to keep the unique attributes of island ecology in mind.

The most ecologically viable and economically efficient invasive species management strategy is always to keep invaders out in the first place. Costs to suppress or extirpate invaders can be astronomical once invaders become widely established and well integrated into a system (Mack et al. 2000, Pimentel et al. 2005). Moreover, even when extirpation of the invader is successful, which is rare on mainlands but increasingly common on islands, residual impacts can sometimes occur that cannot be mitigated. Extinction of a native species is the most obvious of these, but invasive plants can also alter nutrient and soil conditions in ways that leave severe residual effects (Cooks 2002). Thus, establishing monitoring programs for early detection and rapid response to invasions is crucial. Extirpation of nascent populations of invaders is essential to this approach (Moody and Mack 1988, Mack and Lonsdale 2002). Control of small isolated populations can be highly effective (Myers et al. 2000), in part, because extremely powerful tools can be used that would be infeasible for widely established species due to sever side effects. For example, the highly invasive *Caulerpa* seagrass was controlled when first discovered in southern California coastal lagoons by covering the relatively small affected areas with tarps and pumping in chlorine bleach until everything under the tarps, including all native species, were killed (Andersen 2005). Although this treatment was extreme, it was acceptable because after removing the tarp, the bleach dissipated and the site was able to recover through recolonization of natives from the surrounding environment. The method was effective because the localized nature of the invader allowed a severe but potent treatment to be used. This approach obviously could not be applied over the massive area now infected by *Caulerpa* within the Mediterranean Sea (Meinesz 2002) because it would be cost prohibitive and would incur extreme side-effects.

Once invasive species become well-established, it is much more difficult to control or extract them. In this regard, islands have two distinct advantages over mainland systems that have lead to invader extirpation being a primary management goal on islands. First, island size limits the geographic extent of even the most well-established invaders, and second, vertebrate invaders, which present some of the greatest threats on islands, are much more amenable to control than many invasive plants and invertebrates. In the last decade or two, the list of islands from which cats, rats, mice, pigs, goats, rabbits and other vertebrate invaders have been extirpated has grown dramatically and numbers in the hundreds (Veitch and Clout 2002, Nogales et al. 2004, Campbell and Donlan 2005, Howald et al. 2007). Exotic birds are perhaps the most difficult vertebrates to extirpate on islands due to their vagility and high ecological overlap with native avifauna. Successful removal of exotic plants is much rarer, but such successes do occur (Mack and Lonsdale 2002). Successful control of invertebrates on islands is not commonly documented.

In many cases, successful removal of island invaders has allowed for substantial system recovery (Mueller-Dombois and Spatz 1973, Hamman 1979, 1993, Shimizu 1995, Courchamp et al. 2003, Nordstrom et al. 2003), but this is not always the case. Invasive species management can result in unexpected outcomes for several reasons. First, management tools inevitably have side effects on nontarget species. This is because few management tools are so precise as to only affect the target pest. For example, herbicides used for weeds also suppress certain native plants, with potentially long-term effects at the species and community levels (Crone et al. 2009, Rinella et al. 2009, Ortega and Pearson in press). Likewise, poisons used to extirpate rodents on islands can directly affect other consumers and enter into the food chain (Howald et al. 2007). Second, even if management actions are precisely executed such as shooting vertebrates or use of target-specific biological control agents, nontarget species and system components can still experience side effects due to interactions associated with altering species composition in complex systems. In general, the longer an exotic species has been established and the broader its distribution, the more likely its removal is to have complicated outcomes. For instance, over time ecological replacement can occur (sensu Pearson and Callaway 2003, see also Zavaleta et al. 2001), wherein invaders can become heavily integrated into native food webs and ecosystem processes, taking on the ecological roles and functions of native species. When this happens, extirpation or control of the invader can actually threaten native species that have become dependent on the invader or ecological processes driven by the invader. This can happen on mainland systems as illustrated by the controversial control of exotic saltcedar (*Tamarix* spp.), which is used for nesting habitat by bird species of conservation concern in the southwestern United States (Sogge et al. 2008), but islands are particularly prone to this situation due to low functional diversity. Finally, multiple invaders can also greatly complicate control. In the simplest case, control of one exotic species may result in its immediate replacement by another ecologically similar exotic, a situation referred to as secondary invasion in the case of invasive plant management (Pearson and Ortega 2009). Similarly, herbivore removal from islands may fail to result in recovery of the plant community if exotic plants are present that respond more strongly than the native vegetation (Donlan et al. 2003). Moreover, multiple invaders representing different trophic guilds can be particularly problematic, especially on islands, where the invasive species may be the only representative from a key functional group. For example, control of exotic predators on islands where exotics also make up midlevel predators, omnivores, or herbivores can result in dramatic release of lower-level invaders with catastrophic effects (Rayner et al. 2007, Bergstrom et al. 2009).

Invasive species management has historically focused on controlling or extirpating the target pest under the assumption that this will restore the system to its natural state (Pearson and Ortega 2009). However, simply controlling or removing the target species does not necessarily restore the system for the many complex reasons described above. Although islands are in some ways more conducive to successful invasive species management, in other ways they are more sensitive to management side effects. Extirpating exotic species from islands can be costly and requires commitment and follow through for success (Courchamp et al. 2003, Campbell and Donlan 2005, Howald et al. 2007). It also requires a careful understanding of exotic and native system components and the interactions that link them. In particular, when multiple species of exotics are present and include trophic linkages, great care must be taken to remove the right species or species complex in the correct order to ensure success and avoid dire side effects (Bergstrom et al. 2009). Additionally, an important future step in ensuring system recovery will involve post-extirpation follow-up work. For example, efforts to control exotic plants following herbivore removal could greatly enhance system recovery. The progress made in invasive species management on islands over the past two decades is substantial. Refining these techniques by infusing more community- and system-level understandings will greatly improve invasives management on oceanic islands to enhance the protection of these biological treasures.

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■ 주요 경력 *Experience Summary:*

2005년 박사학위를 받은 후부터 현재까지 몬태나주 미줄라에 위치한 미국 산림청(USFS) 산하 로키산맥 연구 스테이션(RMRS)의 생태학자로 근무하고 있다. 현재 야생동물 및 육상 생태계 프로그램의 침입 생태팀과 침입종 대책반 팀장으로 활동하고 있다. 또한 몬태나대학교의 생명과학부에서 객원교수 및 대학원위원회 의장으로도 참여하고 있다. 최근 공학 및 과학 분야 미 대통령상(PECASE)을 수상한 것을 비롯하여 많은 수상 경력이 있으며, Open Ecology Journal의 부편집장으로도 활동하고 있다. 그의 주요 연구 관심분야는 침입 및 군집 생태학이다. 조류학과 관련해서는 탐조활동에 참여할 뿐 아니라, 현재 생물방제나 살충제 등 외래 종자의 관리가 자생하는 명금류에 미치는 영향을 조사하고 있다.

Since completing his PhD in 2005, Dr. Dean Pearson has been a Research Ecologist with the United States Forest Service, Rocky Mountain Research Station (RMRS), located in Missoula, Montana. He is currently Team Leader for the research station's Invasive Species Working Group and the Invasion Ecology Team of the Wildlife and Terrestrial Ecosystems Program. He also serves as faculty affiliate with the University of Montana's Division of Biological Sciences, where he chairs and participates on graduate student committees. Dr. Pearson has received numerous awards, including most recently the Presidents Early Career Award for Engineering and Science (PECASE). He is an associate editor for the Open Ecology Journal. His primary research interests are invasion and community ecology. His ornithological interests include recreational birding, and he is currently involved in studies examining the effects of exotic weed management such as biological control and herbicides on native songbirds.

■ 학력 *Education:*

- 2005: PhD in Organismal Biology and Ecology, University of Montana, MT, USA
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- 1992: BS in Wildlife Biology, University of Montana, MT, USA

■ 주요 저서 및 논문 *Selected Publications:*

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