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Islands

Biological Diversity and Ecosystem Function

With 17 Figures

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18 Experimental Studies on Islands

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18.1 Introduction

As we seek to understand the relationship between biological diversity and ecosystem processes, we often turn to islands because of their unique biota – impoverished, disharmonic, and alien-infested though it may be, there are still those who love it. Islands can be viewed as natural experiments, and ecosystem processes thereon can be compared with those on continents or other islands having similar geology, topography, and climate. Such comparisons should do much to elucidate the relationships between biota and fluxes of materials and energy, as described in Chapter 14.

Nevertheless, island-continent comparisons and natural experiments (Bowden, Chap. 17, this Vol.) are not the only motivations for turning to islands to evaluate biological diversity and ecosystem processes. For a number of reasons, islands lend themselves to experimentation, and the description of such experiments was the task of this working group.

18.2 Advantages of Islands

First among the attractions of performing experiments on islands is the fact that island biota are often well known, and this makes it possible to evaluate gains and losses of species using censuses. Such censuses have been used many times during the development of island biogeography as well as the polemics associated with their applicability to conservation biology.

A second attraction of islands as locales for experiments concerns the opportunity they afford for assessing the functional consequences of harmony and disharmony in their biological spectra (i.e., the degree to which the frequency distribution of taxa on an island corresponds to that of its donor continents). The characteristically skewed spectra of island biota can arise in two ways. In some cases, the biota is disharmonic because some representatives never arrived. In other cases, biological spectra have been modified, often by extinctions associated with the arrival of humans (see James, Chap. 8, this Vol.). In any event, island communities could be subjected to additions and removals at any of several

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levels – species, life-forms, functional groups, or trophic levels. Communities might be reassembled using species from a variety of sources. One such source could be the ecotypes or functional groups that have developed within taxa that have undergone ecological release, such as the multiple forms of a single species (e.g., *Metrosideros polymorpha*) or a larger taxon, such as a family (e.g., Asteraceae; see Eliassòn, Chap. 4, this Vol.). Depending on the objectives of the experiment, reassembly could be restricted to certain groups, such as indigeneous species or utilitarian species. Still another approach would be to run a disharmony experiment in reverse; this would involve leaving the island biota as-is, and experimentally creating, through selective removal of species, equivalent disharmony on a continental system. Responses would be evaluated both by measuring the consequences of the treatment on the continent and by making island-continent comparisons.

A third attraction of island experiments is that they lend themselves to measurement of ecosystem processes. Fluxes of species, mentioned above, are one category of response that can be measured relatively more easily on islands than on continents. The same is true of biogeochemical linkages between contiguous ecosystems. As one example, fluxes of materials across the land-sea interface have important impacts on islands because of their high ratio of edge to surface area. For another, many low-elevation islands are underlain by limestone that contains freshwater lenses, and the reciprocal flows of water, nutrients, and contaminants between the surface and these pockets of freshwater are more readily measured here than on more geologically complex continents.

Finally, despite their common characterization as abused landscapes, the fact remains that some islands – particularly those that are very remote, very small, and free of freshwater – are as pristine as any equal-sized territory on a continent. Clearly, experiments to be performed on these microcosms should be designed to ensure that they do not have lasting impacts on the natural state that makes them such attractive targets for research in the first place.

18.3 Examples

Nine categories of experiments are briefly outlined in Table 18.1 and in the paragraphs below. These sample experiments (not dèfined here with proposal-quality rigor) are included as guideposts to the kinds of issues that would lend themselves to experimental science on islands.

18.3.1 Within-Ecosystem Processes

Some experiments on islands would lead primarily to insights about the relationship between biological diversity and ecosystem processes in the ecosystem subjected to manipulation. As an example, under the general topic of making amends for extinctions, scientists might choose substitutes for extinct species based on a number of criteria, some of which include geographic proximity,

Table 18.1. Examples of the kinds of issues related to biological diversity and ecosystem processes that might be addressed by experiments on islands

General topic	Prediction	Experiment	Biodiversity components	Ecosystem processes
Making amends for extinctions	The ecological role of an extinct species can be reinstated through introduction of a functional, rather than a taxonomic, replacement	Introduction of replacement species on paired islands – one with complete range of biota and functions, one with both degraded	Multispecies interactions such as pollinations, seed distribution, predation, and symbioses	Primary productivity, vegetation dynamics, nutrient and hydrologic cycles, and organic matter dynamics
Loss of functional groups	Productivity will decline with removal of plants that are either habitat specialists or generalists, with specialists responding most at gradient extremes and generalists most midway along the gradient	At several sites along an environmental gradient do two treatments involving removal of (1) dominant habitat generalists, and (2) dominant specialists (plus controls for removal disturbance and no removal)	Functional groups related to environment	Productivity at levels of community and functional groups
Volcanic soil age gradients	Impacts of introduced nitrogen-fixing species are inversely proportional to substrate age and proportional to archipelago distance from continental landmasses	Plant or eliminate exotic N_2-fixer on soils of different age, e.g., different lava flows (same island or archipelago), and on archipelagos varying in isolation from continental landmasses	Nodule-inducing microbes; herbivores; native flora	Nitrogen cycling; growth and survival of coexistent plant species
Islands as nutrient concentrators	Manuring by seabird droppings increases primary productivity	On island edges, select pairs of plots that vary widely in primary productivity; add guano or fertilizer to one plot of each pair	Seabirds and marine mammals; terrestrial plants and animals	Primary productivity, rates of decomposition, mineralization, numbers of herbivores
Trees as condensation nuclei	Trees augment water inputs to dry islands exposed to trade winds	Plant trees (e.g., *Pinus canariensis*) on one member of paired watershed or islands that receive similar rainfall; measure rain in clearing and in plantation; measure throughfall and stemflow	Local flora	Hydrology (driven by total water inputs as sum of rain, throughfall, and stemflow)

Table 18.1. (Contd.)

General topic	Prediction	Experiment	Biodiversity components	Ecosystem processes
Mangrove recovery	Species-rich mangrove forests are more resilient than species-poor stands	Kill groups of trees or stands along mangrove diversity gradients (which may be related to typhoon-frequency gradient across islands)	Mangroves and animals dependent on mangrove communities	Colonization and growth rates of mangrove individuals; production of birds, insects, fish, and root epifauna
Mangrove mortality	Individual tree mortality prevails in species-rich mangrove areas, while stand-level dieback or mass mortality prevail in species-poor mangrove areas	Establish large, permanent inventory plots in many mangrove stands that differ with respect to diversity. Await natural mortality, including that caused by episodic agents such as typhoons	Mangrove species diversity; animals dependent on mangrove communities	Mortality and growth of mangrove individuals
Soil erosion	A diversity of plant species increases canopy density, thereby reducing the erosive impact of rain	Create diverse and simple plantations on deforested lands similar in aspect, soil, topography, and rainfall	Plant species, both native and alien	Runoff amount, rate, sediment load; character of erosion (sheet, rill, gully); infiltration, especially as related to litter quality and quantity
Ecological economics of islands	A subsistence index, defined as the ratio between outside "industrial" inputs and the island's internal capacity for self-maintenance, is inversely proportional to the integrity of the native biota	Choose paired islands in the same archipelago that differ, due to historical reasons, in the degree to which the economy is dependent upon outside inputs. Construct energy (and money) budgets of each, and attempt to reconstruct time course of subsidy in relation to status of natural ecosystems on each	Fraction of land covered by vegetation; fraction of land covered by native plants; sea bird colonies	Primary productivity of terrestrial systems; nutrient return from sea to land via biological pumps; detritus flux from land to sea; productivity of inshore marine systems

islands	island's internal capacity for self-maintenance, is inversely proportional to the integrity of the native biota	reasons, in the degree to which the economy is dependent upon outside inputs. Construct energy (and money) budgets of each, and attempt to reconstruct time course of subsidy in relation to status of natural ecosystems on each	by vegetation; fraction of land covered by native plants; sea bird colonies	return from sea to land via biological pumps; detritus flux from land to sea; productivity of inshore marine systems

taxonomic affinity, ecological similarity, and human acceptability. In addition to the impacts of these introductions on ecosystem processes, it would also be informative to measure the functional properties of the substitute, such as its physiology, behavioral ecology, and phenology.

There could be a number of consequences of adding or deleting functional groups. These might include the acceleration, deceleration, or stagnation of succession; increased or decreased resistance, and responsiveness to pest attacks; absolute and relative changes in primary and secondary productivity; and changed vulnerability to fire. Using the degree of habitat specialization among plants, it may be possible to assess the effects of diversity on ecosystem processes through species removal or revegetation experiments.

Many islands are volcanic, and volcanism (especially in island arc systems derived from hot spots) creates sharp gradients in substrate, upon which other environmental factors are relatively uniform. This leads to a unique opportunity for replicated experimentation involving limiting factors and their changes over time. Furthermore, such comparisons can easily be expanded to accommodate comparisons across archipelagos as well as between islands and continents.

18.3.2 Larger-Scale Phenomena

Other island experiments would lead primarily to insights about the relationship between biological diversity and ecosystem processes at the level of the island and the larger land- and sea-scape of which it is a part. For instance, many islands are focal points for sea-to-land transfer of nutrients via birds, which harvest secondary productivity from vast areas of ocean, and deposit guano on land. A first logical step might involve elimination of an exotic predator, such as the feral cats that are so common on islands that once supported huge colonies of seabirds. Such a program should only be undertaken after first considering possible cascading or linked effects: what will become of exotic rat populations in the absence of cats, and what implications does this hold for the island's biota?

Experiments with coastal fringe ecosystems, such as mangroves, might not require inflicting more damage on these already-battered communities. Instead, they could be implemented by taking advantage of manipulations that have already been induced by development, such as urbanization, agriculture, aquaculture, and drainage for mosquito control, or by using manipulations anticipated or proposed for other purposes, such as mangrove silviculture. As both bridges and barriers between land and sea, coastal fringe ecosystems are linked to processes that merit special attention, such as reef eutrophication, storm penetration, and impacts on detrital food chains of estuaries.

Soil erosion is a response of interest in many kinds of biodiversity experiments, but it is of special significance on islands because of their high edge-to-surface ratio; its potential impact on the inshore marine systems on which the island's human inhabitants may depend for food; and the fact that islands seem to suffer disproportionately from devegetation and the soil erosion it provokes. Biologists should not overlook the economically useful and visible role that native species' conservation and reintroduction can play in controlling erosion.

It may also be useful to scale up from biological systems to the level of ecological economics, for nowhere is the interdependency between humans and their surroundings any tighter than on islands (Defoe 1862). To accommodate this perspective the concept of biodiversity might have to be expanded to include the diversity of human enterprises. Likewise, the concept of an "experiment" might have to be relaxed, although this does not make the research any less crucial, just more difficult. Ecosystem processes, in this case, might imply inputs and outflows tied to human activity, such as economic subsidies, transportation and marketing, capture and use of freshwater, waste disposal, and harvesting (both commercial and subsistence) of products from the surrounding marine ecosystem.

18.4 Conclusions

Well-known, relatively species-poor biota, coupled with well-defined environments not confounded by drastic cross-gradient changes in other factors, make islands excellent settings for experiments on the relationship between biological diversity and ecosystem processes. The main attractions of islands for ecological research are likely to remain the unplanned experiments and island-continent comparisons laid out by their singular environment and unique biogeographical history.

Nevertheless, the superimposition of investigator-imposed treatments on an island's matrix of natural experiments would be a powerful lever in maximizing information yield. Investigators could regard subdivisions of island gradients as experimental blocks, to which further experimental treatments can profitably be added. Islands, as mesocosms of larger-scale phenomena, provide unique, straightforward combinations of organisms and environment, and much can be learned by their manipulation.

Reference

Defoe D (1862) The adventures of Robinson Crusoe. S O Beeton, London