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Theory and design of nature reserves

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Theory and Design of Nature Reserves

Managing landscapes

In a 2008 review, David Lindenmayer and a long list of distinguished conservation biologists review two decades of research on landscape management [5]. They identify a set of 13 factors that anyone managing a landscape for conservation should consider, and they group those factors under four boad themes: setting goals, spatial issues, temporal issues, and management approaches.

- Setting goals
  - Develop long-term shared visions and quantifiable objectives.
- Spatial issues
  - Manage the entire mosaic, not just the pieces.
  - Consider both the amount and configuration of habitat and particular land cover types.
  - Identify disproportionately important species, processes, and landscape elements.
  - Integrate aquatic and terrestrial environments.
  - Use a landscape classification and conceptual models appropriate to objectives.
- Temporal issues
  - Maintain the capability of landscapes to recover from disturbances.
  - Manage for change.
  - Time lags between events and consequences are inevitable.
- Management approaches
  - Manage in an experimental framework.

– Manage both species and ecosystems.
– Manage at multiple scales.
– Allow for contingency.

That set of factors pretty well covers the issues conservation managers have to consider in a large-scale conservation project but there's one task for conservation managers that neither this list nor our discussion so far has dealt with explicitly — designing a conservation reserve system.[1]

Goals of a conservation reserve

By now you're probably tired of hearing me say harp on this them, but the first task in designing a reserve must be to decide what that reserve is *for*—an example of my "If you don't know where you're going you'll probably end up somewhere else" principle. So what *are* the goals of a conservation reserve? Soulé and Simberloff [14] identified three possible goals:

1. Conservation of large, intact, functioning ecosystems,

2. Conservation of areas with high biological diversity, and

3. Conservation of species or groups of species of special interest.

To these three reasons, I would add two more:

4. Conservation of significant natural communities.

5. Conservation of important ecosystem services.[2]

Large, intact, functioning ecosystems

- Sequoia and Kings Canyon National Parks in the Sierra Nevada only protected the giant sequoia (*Sequoiadendron giganteum*) incidentally. They were established to protect an important watershed providing irrigation water for farms in the Central Valley. Yellowstone and Yosemite were established largely because of the unique geological features of the first and the scenery of the second.

[1] Actually, that's not quite fair. Lindenmayer et al. [5] do mention "managing the entire mosaic" and "considering both the amount and configuration of habitat".

[2] Which is close to #1 but not identical.

- To protect an intact functioning ecosystem, the area protected must be *very* large. Yellowstone and Grand Teton National Parks together have an area about the size of the state of Connecticut. An area of this size seems just large enough to contain a viable population of grizzly bears. According to the National Park Service, there were at 97 wolves in 11 packs (6 were loners) Yellowstone National Park at the end of 2010 (http://www.nps.gov/yell/naturescience/wolves.htm).[3]

- Protecting these vast expanses is the only hope we have for saving large-bodied mammalian carnivores, and there are few places in the world where this is possible. It's also pretty clear that there are large areas of the continental United States where it is no longer possible to set aside such areas (Figure 1)

Areas with high biological diversity

- Rainforest preserves in the rainforest come immediately to mind, but also Madagascar, coral reefs.

- Norman Myers and Conservation International [9] have championed a "hotspot" approach: "as many as 44% of all species of vascular plants and 35% of all species in four vertebrate groups are confined to hotspots comprising only 1.4% of the land surface of the Earth."

- A little *good* news for a change. A concentrated effort in a few high priority areas can, with careful long-term management, ensure that a large proportion of the world's biodiversity will survive us.

- We see the same phenomenon at a smaller scale. Dobson et al. [3] compiled a database recording county-level occurrences of all plants and animals protected under the Endangered Species Act as of August 1995. Using this database they used a sorting algorithm to identify "hot spots" for endangered species for amphibians, arachnids, birds, clams, crustacea, fish, insects, mammals, plants, reptiles, and snails.

    1. Select the county with the greatest number of endangered species. In the case of a tie select the county with the smallest area.
    2. Exclude all species found in that county from further consideration.
    3. Return to step 1.

[3] Wolves were re-introduced to Yellowstone in 1995 and 1996. The number at the end of 2010 is down slightly from 2008 when it was 24 wolves in 12 packs.

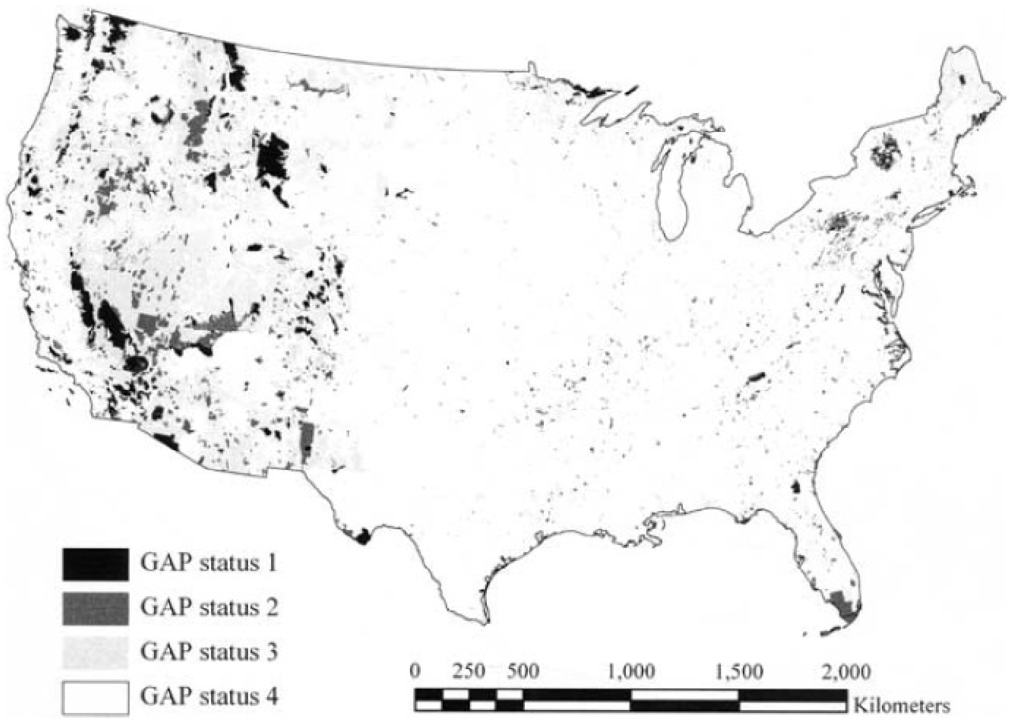

Figure 1: Conservation status of lands in the continental United States. Gap status 1 – areas with permanent protection. Gap status 2 – areas with permanent protection, but management that degrades natural communities is allowed. Gap status 3 – areas with permanent protection but subject to resource extraction. Gap status 4 – areas without known public or private mandates for protection. (From [2]).

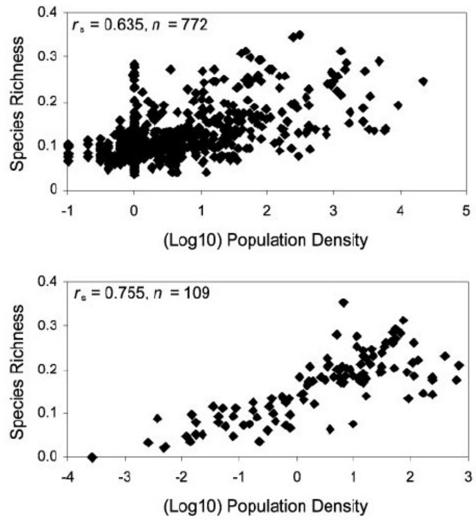

Figure 2: The relationship between human population density and species richness in Australia (upper) and the United States (lower) (from [6]).

More than 50% of endangered species in each group are represented with between 0.14 and 2.04% of land area.

- Of course things never turn out to be quite as simple as they first seem. Luck et al. [6] point out that there's a positive correlation between *human* population density and species richness (birds, mammals, reptiles, amphibians, and butterflies) in both Australia and the United States (Figure 2), with the exception of reptiles in Australia. In other words, the places that would be the highest priority for conservation in terms of species diversity are also the places where the most people live and setting aside land for conservation will be most difficult, controversial, and expensive.

- Fortunately, there's still some good news in the end. Suppose we set as a conservation goal representing each species at least once and choosing the smallest set of grid cells (or the grid cells that would cost the least to acquire) that allow us to do that. Then compare what happens under two scenarios: (1) ignore human population density (effectively assuming all grid cells are equally costly) and (2) assign each grid cell a cost proportional to human population density. What you see is that under the second strategy, overlap can be largely avoided (0% to ca. 10% depending on the taxonomic group) and that the total area required for conseration is only slightly

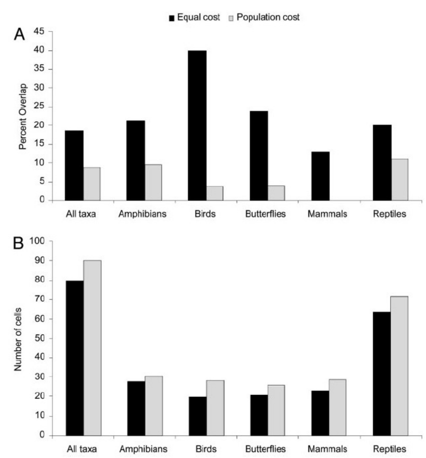

Figure 3: Percent of overlap between conservation targets and human population density under the two scenarios (a) and the number of grid cells included in the conservation targets under the two scenarios (from [6]).

greater (Figure 3).[4]

- Although these ideas are promising, we'll see next week that there are some reasons why a "hotspot" approach to setting conservation priorities may miss some important conservation objectives.

Significant species and natural communities

- Spotted-owl and marbled murrelet
- Serpentine outcrops on the Tiburon peninsula north of San Francisco—*Calochortus tiburonensis.*

Soulé and Simberloff left out another important function of nature reserves to my mind. In a way it's implicit in the first purpose, but it need not be carried out at the very large scale that conservation of large, intact, function ecosystems implies.

- In developed parts of the world, like Connecticut and most of the eastern seaboard, no large, intact ecosystems remain to be protected. What we can do is protect pieces

[4]Overlap is defined as occurring when a grid cell required for conservation corresponds to a grid cell in the top decile of human population density.

of what is left, even if those pieces are not particularly diverse. Salt marshes, the rocky intertidal, red maple swamps, and sphagnum bogs, for example. None may be especially diverse and they may harbor few globally endangered species, but the species they represent important elements of natural diversity that I, at least, would hate to lose. Moreover, they often represent the first, or only, exposure that those in urbanized areas have to places that are a little bit wild. As a result, they may be critical to ensuring that future generations develop an appreciation for parts of the world other than shopping malls.

Introduction to reserve design

Once we've determined what purpose our reserve system is supposed to serve, there are, as I see it, five questions to be answered in producing a preserve design.

1. What are the elements[5] of concern?
2. Where are the elements of concern found?
3. How large must the reserve be to serve its purpose?
4. What features of the reserve must be protected/managed to allow the elements to persist in the area, e.g., patch dynamics, landscape context?
5. How large a buffer zone is required to prevent/reverse degradation of the primary habitat?
6. How does this reserve fit into a system of conservation reserves? Is it a stand-alone reserve? If not, how ought the size, number, and spatial configuration of reserve components to be selected?

Once these decisions have been made, many other decisions must be made about exactly how the land is to be protected—whether by purchase, conservation easement, partnership agreement, etc.

The design of reserve systems involves a "representation problem," i.e., finding a configuration of reserves that ensures all elements of concern are "represented."[6] Formal approaches to solving these problems are often described in terms of minimizing either the number of areas to be protected or the total area of areas to be protected. Pressey et al. [12], for example, identify four problems for which solutions might be required:

[5] *element*—a species, natural community, or ecosystem component.

[6] We saw an example of this in the Luck et al. [6] study.

1. Identify the minimum number of sites needed to represent at least one occurrence.[7]

2. Identify the minimum total area of sites needed to represent at least one occurence.

3. Identify the minimum number of sites needed to represent at least 5% of the total regional extent.[8]

4. Identify the minimum total area of sites needed to represent at least 5% of the total regional extent.

In the test application they describe, Pressey et al. seek to ensure representation of 248 land systems[9] across 1885 potential conservation sites in an area of 325,000 km^2. They find that a minimum of 54 sites (2.86% of the total) and an area of 12084 km^2 (3.72% of the total) are needed to represent at least one occurrence of each land system. They find that a minimum of 126 sites (6.68% of the total) and an area of 25887 km^2 (7.96% of the total) is needed to represent at least 5% of each land system.

As complicated as this may seem, Ando and Mallory [1] point out that in many circumstances the approach I've just described isn't sufficient. Consider the problem of how to allocate efforts to conserve prairie potholes among the eastern, central, and western regions of their distribution in the face of climate change. There's a good measure of wetland habitat quality available, the cover-cycle index (CCI), and the expected value of CCI has been estimated not only under current conditions, but also under a warming of 2°C, a warming of 4°C, and a warminng of 4°C plus an increase of precipitation by 10 percent. The problem is that we don't have a good idea of what's going to happen. At best we can specify probabilities (Table 1), and since we don't even know well what those probabilities are, they consider two different sets of probabilities: the "no change likely" set and the "uniform" set.

So how do we allocate resources among the three regions taking into account this information? Remember long ago when I told you that there were lessons from population viability analysis that apply to your investment portfolio, namely that you have to worry not only about mean population growth rate but also its variance. Well, folks in finance have been aware of this for more than 60 years. They recognize that there's generally a tradeoff between risk and return. If you want to have a high expected rate of return on your investments, you have to be willing to live with quite a bit of uncertainty. What you don't want to do is to have a lot of uncertainty and a low return. This led to the idea of an

[7]**Note**: The principle is the same if we decide that we want to ensure that each element is represented more than once.

[8]**Note**:The principle is the same if we decide that we want to ensure representation of some other fraction of the total regional extent.

[9]Land systems are defined as "recurring patterns of landform, soil, and vegetation."

	no change	$+2°C$	$+4°C$	$+4°C$, wetter
Probabilities of climate outcomes				
No change likely	0.80	0.10	0.05	0.05
Uniform	0.25	0.25	0.25	0.25
Average wetland habitat quality (CCI)				
Western	0.290	0.178	0.124	0.168
Central	0.718	0.587	0.251	0.503
Eastern	0.317	0.561	0.584	0.654
Average conservation cost (in $1000 per acre)				
Western	$0.601	$0.631	$0.631	$0.536
Central	$0.697	$0.720	$0.720	$0.659
Eastern	$1.21	$1.23	$1.23	$1.20

Table 1: Parameter values for different climate change scenarios in the prairie pothole region (from [1]).

"efficient frontier" (Figure 4). As you can see, a simple diversification approach that divided efforts equally among the regions does significantly worse under either set of probabilities. For the same amount of risk a higher return is possible. Alternatively, the same return is possible with a smaller amount of risk.

In addition to deciding on the size, number, and spatial configuration of units to be included in a conservation reserve system, conservation managers must make several additional layers of decisions:

- How frequently must the status of populations/communities be monitored?
- Is it necessary to manipulate the habitat to, for example, preserve early successional environments?
- Should an effort be made to exclude/remove invasive exotics?

We won't talk specifically about these questions, since we've been talking about them all semester. Besides, there are few, if any, general principles that can be applied to all reserves. Rather, good biological judgement based on the best natural history information available is always required, as is a clear sense of what the priorities are.

In designing nature reserves there's a lesson from landscape ecology that is especially important to remember. I suppose you could call it ecology's relativity principle:

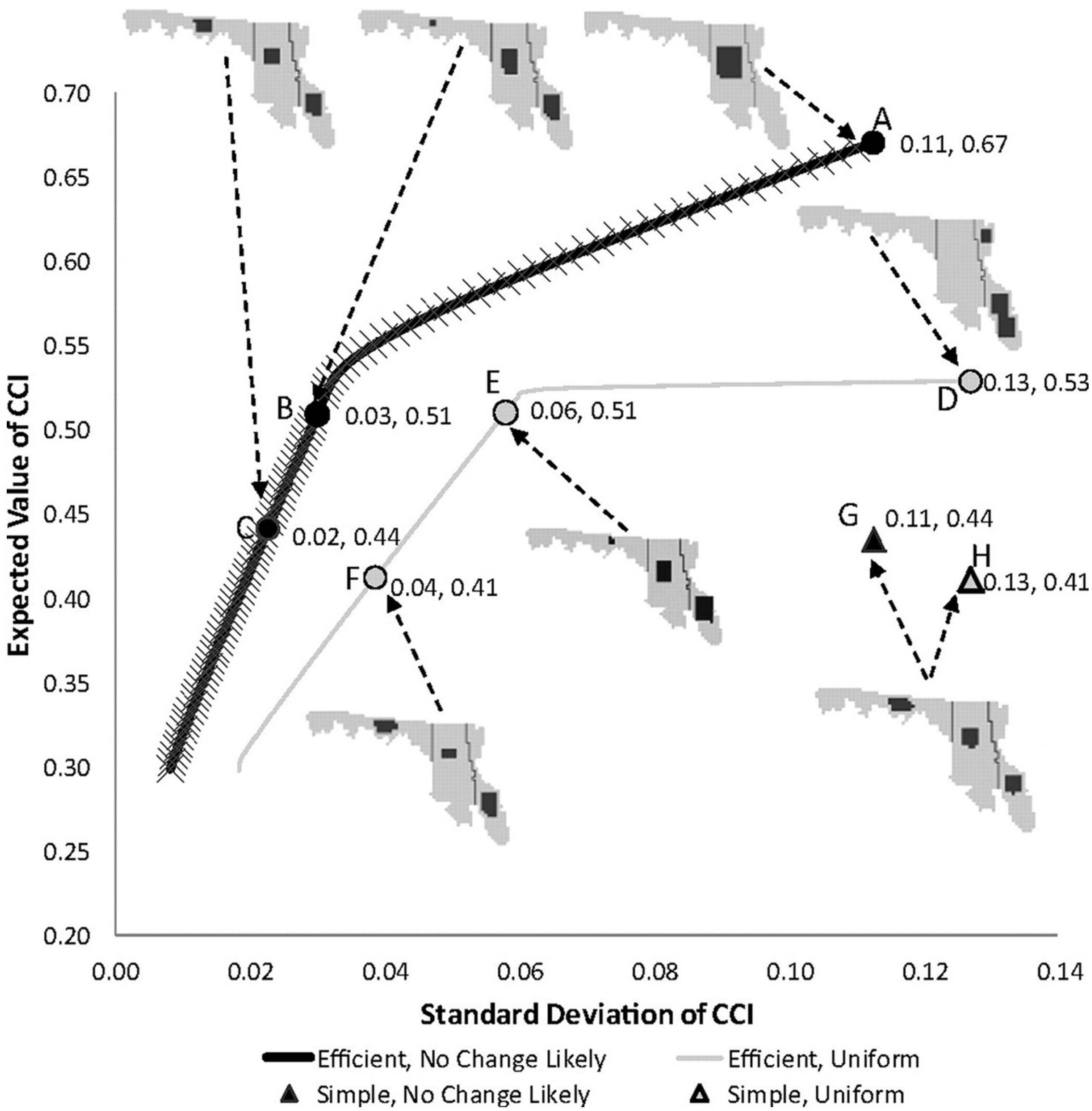

Figure 4: The "efficient frontier" for allocating resources among three regions of prairie potholes in the "no change likely" (bold line) and "uniform" (light gray line) (from [1]).

- There is no single, universally applicable spatial or temporal scale appropriate for understanding all ecological processes. The scale that is appropriate depends on the process you are trying to understand.
  - Population dynamics of *Arabidopsis thaliana* vs. population dynamics of *Quercus rubra*

The application of this principle to design of nature reserves is quite straightforward:

- There is no single size, no single scheme of management, no single means of protection that is universally applicable to all conservation reserves. The appropriate size, the appropriate management scheme, and the appropriate means of protection depend on the purpose for which the reserve was established.

Unfortunately, we don't have time this semester for a lecture focusing specifically on landscape ecology and remote sensing, but let me mention a few principles that might have been covered in such a lecture that are especially relevant to design of reserves or reserve systems:

- Remote sensing—Landsat thematic mappers, SPOT, and all that—means that it is now possible to use very sophisticated techniques to identify areas of conservation concern and the threats to which they may be subject—assuming[10] that the elements of conservation concern can be associated with data derived from remote sensing, primarily vegetation cover and land use.
- The middle level of spatial and temporal scales—those that span decades or centuries rather than millenia and areas from a few hectares to a few tens of square kilometers—are often the most relevant for conservation purposes, at least in highly developed parts of the world. The opportunities for conservation at the scale of hundreds or thousands of square kilometers are relatively few.[11]
  - They are the time scales over which many ecological processes happen, and especially those ecological processes over which human beings may hope to have some influence.

[10] And it's a *big* assumption

[11] Or at least they're few if we're thinking in terms of traditional conservation reserves. They are abundant if we think about managing ecosystems in which humans are an integral part of the system.

  - They are the spatial scales over which management schemes can have a direct impact.[12]

- Gap analysis—A national program using remote sensing data to identify "gaps" in conservation coverage. Quoting from their web page `http://gapanalysis.usgs.gov/about-gap/who-we-are/`:

  > The Gap Analysis Program (GAP) is an element of the U.S. Geological Survey. We help implement the Department of Interior's goals of inventory, monitoring, research, and information transfer. GAP has three primary goals:
  >
  > 1. Identify conservation gaps that help keep common species common;
  > 2. Provide conservation information to the public so that informed resource management decisions can be made; and
  > 3. Facilitate the application of GAP data and analysis to specific resource management activities.
  >
  > To implement these goals, GAP carries out the following objectives:
  >
  > - Map the land cover of the United States
  > - Map predicted distributions of vertebrate species for the U.S.
  > - Map the location, ownership and stewardship of protected areas
  > - Document the representation of vertebrate species and land cover types in areas managed for the long-term maintenance of biodiversity
  > - Provide this information to the public and those entities charged with land use research, policy, planning, and management
  > - Build institutional cooperation in the application of this information to state and regional management activities.
  >
  > GAP conducts national as well as regional and state projects, utilizing cooperative efforts among federal, state and regional agencies and private organizations.

Nature reserves have often been established, at least by private organizations like the Nature Conservancy, for the protection of identifiably rare and endangered species. In

[12] At scales smaller than a hectare or so, stochastic changes become almost unavoidable and may dominate the dynamics. At scales larger than a few tens of square kilometers it is difficult to have any impact on the whole system, except to the extent that actions like reducing the output of greenhouse gases affects *all* systems on the planet.

so doing, they may have failed to help prevent the general biotic impoverishment that accompanies the conversion of natural ecosystems to human-dominated ones. The importance of gap analysis is less in its conceptual novelty than in the emphasis it helps to place on protection of diverse ecosystems, even if that diversity is composed primarily of non-endangered species. It is also a systematic, *planned* attempt to put together a system of reserves that make sense, rather than making piecemeal decisions on individual pieces of property.

Problems with a focal species approach

There is a large potential problem, however. The Gap Analysis program presumes that vegetation cover and predicted vertebrate distribution will be a good surrogate for diversity in other groups. How likely is this? Well, Prendergast and colleagues [11] looked at the distribution of five groups on the island of Britain:

1. butterflies,
2. dragonflies,
3. aquatic plants,
4. breeding birds, and
5. liverworts.

In a 10km grid that covered all of England, Wales, and Scotland they recorded the number of species in each group.[13] The survey included a total of 2500 tracts. They then ranked separately for each taxonomic group each tract into the 5% with the highest number of species and the 5% with the lowest number of species. How much "hot spot" overlap was there between taxonomic groups?

- Butterflies and birds share only 10% of hot spots.
- Butterflies and dragonflies share 34% of hot spots, the greatest overlap found.
- None of the 2500 tracts is a hotspot for all five groups. Liverwort hot spots are concentrated in western Scotland. Dragonfly hot spots are concentrated in southern England.
- Protecting tracts with a high diversity may not protect rare species. 16% of rare birds were found in *cold* spots.

[13] A similar analysis probably isn't possible anywhere else in the world.

- Dobson et al. [3] did a similar analysis using their data on the distribution of endangered species in the United States.
  - Remember that they divided their data into 11 taxonomic groups.
  - In the 2858 counties included in their study only two are hot spots for three groups: San Diego, California (fish, mammals, and plants) and Santa Cruz, California (arthopods, reptiles and amphibians, and plants).
  - Only nine counties are hotspots for two groups: Hawaii, Honolulu, Kauai, and Maui, Hawaii; Los Angeles and San Francisco, California; Highlands and Monroe, Florida; and Whitfield, Georgia.

You could be forgiven for thinking to yourself that the problem with these studies is that they're looking for overlap between taxa that are *very* different from one another. After all, what competent ecologist would expect liverwort diversity to be associated with butterfly diversity? Well, I have what may be bad news for you. Lindenmayer et al. [4] recently studied how well proposed focal species in Australian birds served as indicators of bird species richness. Specifically, they studied 134 isolated temperate woodlands in New South Wales. The woodlands were found on 45 different farms. They identified five focal species based on published analyses showing that they are indicators of patch isolation, patch area, three kinds of resources (logs, hollow-bearing trees, and mistletoe), or some combination of those factors. There are 155 bird species in the study area, 35% of which are migratory and only 4 of which are non-native.[14]

Surveys of the 134 woodlands in 2002, 2004, 2006, 2008, 2009, and 2011 allowed them to estimate the local species richness in each woodland. They then examined the extent to which focal species indicate local species richness in several ways. We'll focus on one very nice summary of the results (Figure 5).

There are several interesting things about these results.

- Brown Treecreeper seems to be a pretty good indicator of bird species richness.
- There are many species that would serve at least as well as indicators as Eastern Yellow Robin, Hooded Robin, or Mistletoebird.
- Superb Parrot is an anti-indicator, i.e., it is more likely to be found in sites that are species poor than in those that are species rich.

So it appears that in order to pick a good indicator (or good set of indicators), you'd have to have a pretty good idea of what species richness is like in the first place. Is there a place for indicators at all?

[14] Two of the non-native species have declined significantly over the last 10 years.

Species	Spring[a]						Winter[b]					
	Richness quintile						Richness quintile					
	1	2	3	4	5	% change[c]	1	2	3	4	5	% change[c]
Black-chinned Honeyeater	0	1	1	7	12	24	0	2	2	4	10	65
Brown Treecreeper	1	9	20	48	68	51	0	10	18	39	56	69
Buff-rumped Thornbill	0	1	3	5	9	24	2	2	2	3	15	30
Common Bronzewing	2	11	9	16	22	15	1	4	7	15	18	32
Crested Shrike-tit	0	2	6	22	37	35	1	5	1	15	17	38
Diamond Firetail	0	0	4	6	15	28	0	2	0	12	9	50
Dusky Woodswallow	1	3	13	31	41	33	0	1	1	3	6	51
Eastern Yellow Robin	0	0	0	2	11	48	0	2	0	2	6	39
Flame Robin	0	0	0	0	0	—	0	2	14	20	23	37
Fuscous Honeyeater	0	1	1	4	11	36	0	1	0	10	14	68
Golden Whistler	0	0	0	1	3	32	1	4	3	4	16	33
Grey Butcherbird	31	13	7	7	3	-22	16	6	8	3	1	-29
Grey Fantail	0	2	2	4	11	26	1	6	10	10	17	20
Grey Shrike-thrush	4	15	25	47	80	52	2	15	10	44	61	65
Hooded Robin	0	1	3	2	13	32	0	2	0	3	6	51
Jacky Winter	1	5	7	16	33	31	0	7	5	13	30	55
Little Friarbird	1	3	16	23	35	28	0	2	1	4	6	44
Mistletoebird	0	4	5	8	20	22	0	4	5	6	14	34
Noisy Miner	97	86	69	50	32	-27	96	73	70	47	45	-29
Olive-backed Oriole	0	1	1	3	7	35	0	0	0	2	2	57
Peaceful Dove	1	3	9	14	32	34	0	2	3	9	14	37
Red Wattlebird	2	8	19	29	39	26	8	17	19	34	44	32
Restless Flycatcher	0	1	6	16	31	40	1	3	5	15	23	44
Rufous Whistler	1	10	9	18	32	25	0	2	4	2	6	16
Sacred Kingfisher	1	4	5	13	32	29	0	0	0	0	0	—
Scarlet Robin	0	0	0	0	1	—	0	2	1	2	11	51
Silvereye	0	0	0	3	2	26	0	2	0	4	6	32
Superb Fairy-wren	1	3	14	16	32	28	1	6	10	22	31	43
Superb Parrot	28	18	5	12	5	-13	1	2	1	0	0	—
Varied Sittella	0	0	0	0	4	37	0	1	0	0	2	35
Western Gerygone	0	1	5	1	9	21	0	0	1	1	2	30
White-browed Babbler	1	1	3	4	11	20	0	3	1	6	9	42
White-naped Honeyeater	1	1	1	0	4	20	0	2	3	9	16	57
White-plumed Honeyeater	11	38	61	83	93	64	28	50	73	82	91	65
White-throated Treecreeper	1	1	1	9	13	29	0	1	0	2	10	65
Willie Wagtail	9	43	74	84	92	66	21	33	61	64	81	49
Yellow-faced Honeyeater	0	1	1	1	4	26	0	1	1	9	12	54

[a] Quintiles for spring are: 1, < 9.9 species; 2, < 12.0; 3, < 14.0; 4, < 16.9; 5, > 16.9.
[b] Quintiles for winter are: 1, < 7.5 species; 2, < 9.0; 3, < 10.5; 4, < 11.9; 5, > 11.9.
[c] The average percentage increase in odds of occurrence of a species corresponding to an increase of one species in the site-specific species richness.

Figure 5: Average percentage occurrence by species in sites of different species richness and change in odds of occurrence with increasing species richness (from [4]).

A digression into the history of reserve design

So after that long-winded, general introduction I'm going to step back a bit further than I already have from reality, and to talk a little about the history of thinking about reserve design. I do this for three reasons:

1. The theory of reserve design began with applying principles of island biogeography a lá MacArthur & Wilson. It's a good chance to see what is now widely regarded as a false start in conservation biology and how it emerged from a reasonably well-established theoretical and empirical base. It serves as a check to our egos, lest we begin to think that we really do understand everything.

2. The theory of island biogeography is the basis for many of the estimates of contemporary extinction rates that I quoted in my first lecture many weeks ago. It's important to understand where these estimates come from and to get some sense of their reliability.

3. Finally, all though the theory of island biogeography does have limited applicability to the design of nature reserves, there are a couple of important principles that emerge from it that are worthy of consideration.

The Theory of Island Biogeography

One of the most obvious observations you can make about factors affecting species diversity is that the larger the area, the more species it is likely to contain. This was first formalized in the 1920's, but it wasn't until the 1960's that the species-area curve became a serious object of study. Preston [13] and MacArthur & Wilson [7, 8] provided the first explanation for the widely observed power relationship

$$S = CA^z \quad ,$$

where S is the number of species, A is the area, and C and z are species-specific constants. C measures the overall species richness, and z measures the extent to which increases in area have diminishing returns in terms of the number of species. Low values of z indicate strongly diminishing returns. z values tend to vary between 0.18 and 0.35, i.e., to double the number of species the area must be increased by a factor of between seven and 100.

Prior to Preston and MacArthur & Wilson, biologists who worried about the species-area relationship at all tended to explain it simply as a result of the greater habitat diversity associated with larger geographical areas. The equilibrium theory of biogeography proposes another explanation, that the species diversity of an area is the result of an equilibrium between colonization and extinction.

- If we compare large islands with small islands, we expect extinctions less frequently on large islands (because of larger local population sizes). If colonization occurs at the same rate on large and small islands, large islands will support a greater diversity of species.

- If we compare islands close to the mainland (a source of colonists) with those far away, we expect colonizations less frequently on distant islands than on near islands. If extinctions occur at the same rate on near and far islands, near islands will support a greater diversity of species than far islands.

In broad outline, both of these predictions seem to hold. In detail, there are many exceptions. Note, however, that the *equilibrium* theory implies a constant *turnover* in species, i.e., continual changes in species composition. An alternative interpretation of the phenomena is that the patterns seen are not equilibria at all. Even if they're not, they may provide some useful insight for conservationists.

Implications of Island Biogeography

Insularization[15] may have immediate impacts. Some species require large tracts of undisturbed habitat for their continued existence. They may be lost almost immediately from small habitat islands. These are *short-term insularization effects.*

As a result of reduced habitat area, insularization is also expected to lead to loss of local species diversity in the long term.

- Barro Colorado Island was formed in 1914 with the flooding of the Panama Canal. Of the 208 birds that bred on the island prior to flooding, 48 have gone extinct.

- At the last glacial maximum, all of the islands on the Sunda shelf—Borneo, Bali, Java, and Sumatra—were part of a much larger southeast Asian landmass. They were probably separated from the Malay Peninsula (and from one another) by 10,000 years ago. Based on the assumption that the species area curve for the present mainland also applied to the islands when they were part of the mainland, we can calculate how many species have been lost from each of the islands (Table 2).

The loss of species as a result of insularization often referred to as "faunal collapse," reflecting the animal bias of the people who have worked on the problem. Nonetheless, this aspect of island biogeography is broadly accepted, and is the basis for many estimates

[15] *insularization*—the production of islands of habitats, insularization is another name for fragmentation

Island	Area km^2	Initial Number of Species	Present Number of Species	Number of Extinctions	Percent Extinctions
Borneo	751,709	153	123	30	20
Sumatra	425,485	139	117	22	16
Java	126,806	113	74	39	35
Bali	5,443	66	19	47	71

Table 2: Faunal "relaxation" on islands of the Sunda shelf.

of extinction rates.[16] More controversial, and much less certain, is the application of the equilibrium theory of island biogeography to the design of nature reserves.

The SLOSS debate

I mentioned in my opening lecture that much of the early conservation biology literature was dominated by discussion of genetics. Well, much of the literature that wasn't devoted to genetics was devoted to using the theory of island biogeography to design nature reserves—or to disputing its utility. The most heated of these debates even earned its own acronym: the SLOSS debate.

Suppose you had money to purchase 10,000 hectares of land. Assume for the moment that you can ignore all management problems and that your only concern is the spatial configuration of that 10,000 hectares. Would it be better to have a *single large* reserve *or several small* reserves? Would it make more sense to buy a single piece of property 10,000 hectares in extent or 10 pieces of property each of 1,000 hectares?

Early advocates of the use of island biogeography theory, notably Soulé, Wilcox, Terborgh, and Lovejoy, argued that a single large reserve is generally better able to preserve more and larger populations than an equal area divided into a collection of small reserves. They had two reasons for this claim:

- Contiguous areas are better able to preserve intact communities of interdependent species.
- Contiguous areas are better able to maintain viable populations of species that occur at low population densities, especially large vertebrates.

There are at least two problems with these arguments.

[16] If we know the rate at which tropical rainforest is being lost and the species-area relationships typical of a tropical rainforest, we can calculate the rate at which species diversity is being reduced.

- "Largeness" is in the eye of the beholder. For annual plants, for vegetative perennials, and for small, sedentary animals a few hectares may encompass *all* the appropriate habitat, e.g., a peat bog or a serpentine outcrop. Conservationists who want to protect plant diversity, therefore, are probably better off buying several reserves of a few tens to hundreds of hectares in a diversity of habitats, soil types, and geological regimes than buying a single, large reserve of a couple thousand hectares. If you're interested in forest birds, however, small reserves of one or two hundred hectares may not be large enough to support nesting populations.

- As several critics (e.g., Simberloff, Quinn) were quick to point out, island biogeography theory does not require that the species on small islands be a subset of those on large islands. In fact, in a strict interpretation of the *equilibrium* theory, at least, you'd expect them *not* to be subsets. As a result, you might actually save more species in a system of small reserves than in a single large one, even though each reserve would contain fewer species.[17]

- In addition, there were more fundamental criticisms of the approach because there is little evidence that the differences in species diversity on islands is a colonization-extinction equilibrium. Specifically, there is little evidence for species turnover.

To a large extent, however, this whole debate seems to have missed the point. After all, we put reserves where we find species or communities that we want to save. We make them as large as we can, or as large as we need to to protect the elements of our concern. We are not usually faced with the optimization choice poised in the debate. To the extent we have choices, the choices we face are more like those that Pressey et al. [12] describe, i.e., how small an area can we get away with protecting and which are the most critical parcels?

Conclusions

Although in some ways the SLOSS debate may seem like a dead end, there are several important points to remember:

- The suggestion that a single large reserve was preferable emerged from a respectable, legitimate body of ecological understanding. Just as ecologists and evolutionists have often followed blind alleys, conservationists can be expected to. In fact, you could argue that if we don't occasionally make mistakes we are avoiding difficult problems.

[17] It's worth noting that it probably doesn't work this way, but it does illustrate that the management advice from island biogeography theory isn't as straightforward as we might have hoped.

- Reserve designs must serve a purpose. Reserves designed to protect plant diversity may be entirely different in character from those designed to protect vertebrate diversity. Reserves designed to protect exemplary natural communities will have a focus different from those designed to protect an endangered species.

- Reserve designs are more frequently guided by *where* elements of concern occur than by *a priori* theories about the best configuration of preserves. A little common sense, some basic biological and ecological awareness, and a little information about an area allow you to make an informed judgement about where to draw preserve boundaries.[18] Just as importantly, however, we must remember how little information our initial decisions are based on and jump at the chance to change them as new information becomes available.

- Nodes, networks, and MUMs
  - An approach to designing systems of reserves to enhance the effectiveness of the ensemble [10]
  - Node—An area with an unusually high conservation value.
  - Network—A system of corridors to allow movement among nodes, since nodes will rarely be large enough to allow persistence of low-density organisms.
  - MUMs (Multiple Use Modules)—A central, well-protected core surrounded by areas of increasingly greater human impact.

Let's return to the five-step process I outlined earlier:

1. What are the elements of concern?
2. Where are the elements of concern found?
3. How large must the preserve be to serve its purpose?
4. What features of the preserve must be protected/managed to allow the elements to persist in the area?
5. How large a buffer zone is required to prevent/reverse degradation of the primary habitat?

[18]The trouble with common sense, as Voltaire points out in his *Philosophical Dictionary*, is that it is not very common.

You'll notice that the abstract ideas I talked about a few minutes ago acutally play very little role in this list. What that suggests to me, however, isn't that the abstract concepts are useless. If they were, I wouldn't have troubled you with them. What it suggests is that problems are often site-specific (and taxon-specific) and that concrete applications of the abstract concepts will depend on those site-specific features. Furthermore, most of the questions that must be answered during the course of putting together a reserve design must be answered with very little information available. Still, there are several important things to realize:

1. The reserve design is *never* fixed—or at least is *should* never be fixed. It should always be open for amendment and improvement as new information becomes available. New threats to the primary habitat may require larger or more stringently enforced buffer zones. Unexpectedly vigorous population recoveries in target species may lessen the need for interventionist management and monitoring.

2. Even though decisions about reserve boundaries often seem arbitrary and ill-founded—Should we draw the line up this ridge or that ridge?—the results are based on such fundamental properties—soil types and distribution, geological and hydrological features, the geographical location of known populations of species of concern—that even if we were to study an area in detail for fifteen or twenty years, the eventual boundaries that we drew would likely be almost identical to those that we draw based on our "gut" feelings. After all, those gut feelings integrate a *lot* of knowledge and understanding of the natural world—knowledge and understanding that we too often underestimate and undervalue.

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