

JAMES GIBBS

DM: Our last talk in this session, before we have the panel, is and I'm going to move very quickly to it is James Gibbs. And James Gibbs is at the State University of New York, College of Environmental Science and Forestry. And he is going to talk about Range Collapses and the Loss of Genetic Variation within Species.

RANGE COLLAPSES AND THE LOSS OF  
GENETIC VARIATION WITHIN SPECIES

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JG: Thank you very much, Don, and good afternoon. Before I begin, I'd also like to thank the conference organizers for inviting me to speak today on a topic of great interest to me. And one that I think is, perhaps, largely unappreciated in many of our discussions about the biodiversity crisis. And this particular topic is generally related to population declines, and the corresponding contractions that you find in species geographical ranges and distributions. And what the consequences of those processes are for genetic diversity that resides within species.

And what I'd really like to do in the next 20 minutes is just to better frame this issue for you but also to describe a new approach that I've been working on with Don Falk at the University of Arizona, to find ways to its sort of a complicated issue, but find ways to better communicate it to both land managers, collections managers and policy-makers who actually make a difference on the ground.

Just to put this in a larger context, I think, when we're talking about the biodiversity crisis, and what's at stake for the global gene pool, I think the public focuses, and rightly so, on loss of distinct evolutionary lineages; losses of entire species, genera sometimes even families. And I say rightfully so. When those lineages disappear, with them go all of the genetic characteristics that make them unique.

On the other hand, there is another dimension to all this that I think doesn't get much attention at all. And my thinking on this was first stimulated by a brief letter to *Science* that Paul Ehrlich wrote 10 years ago, in which he made the simple point that: A major component of the decline of biodiversity is loss of genetically distinct populations. He actually went on in that same letter to say this was the major, the major issue in the biodiversity crisis. Not just in terms of loss of genetic diversity, but also in terms of ecosystem services across huge areas. Whether you agree with this entirely or not, the point is that it is a legitimate issue, and I'd like to kind of elaborate on that.

Here's what we're talking about and I just chose this as an example organism. You could choose one of many. This happens to be *Plethodon cinereus* the northern red-backed salamander. A fairly limited range in the northeastern United States kind of an obscure little creature. Believe it or not, the most abundant terrestrial vertebrate of our vertebrate species, period, in our environment. They reach tremendous densities up to 5 to 10,000 per hectare in mature forests.

But a nice example. These have You can see there's a lot of variation in just color morphs alone, across the range. And some of these occur in the same population, though many of them are actually unique to particular

populations in different parts of the species range. And allozyme studies have shown that these have among the highest levels of divergence of any species reported.  $F_{ST}$  s on the order of .5 and even .8, when you look across their entire range.

Exactly what determines how much divergence and how genetic variation is distributed within species is complicated. It's a product of many different factors. Certainly, selection regimes and local adaptation mediated, to varying extents, by the amount of gene flow occurring across the species range and among populations. And certainly rates of mutation.

In some groups, timing and degree of reproductive isolation, particularly in plants, can certainly accentuate the amount of divergence you find among populations within species. And, most bewildering of all, is sort of historical events that are very hard to piece together, relating to founder events, bottlenecks, genetic drift in small populations. But these are basically the driving forces that determine the variation that occurs within species how it's distributed across a species range.

Why be concerned with this issue? I get asked that fairly regularly. I think you can argue natural selection can't really occur if there's not genetic variation to work with, to begin with. And, certainly, we're seeing rapidly changing environments fragmentation, climate change. And the way I like to think about it the neutral variation of today is, to some extent, a preadaptation to unknown environments of the future. And retaining that variation is basically retaining the evolutionary potential of species and populations to change.

From a purely selfish perspective, many, many examples of how genes from wild relatives are an important source of material for improving, reinvigorating even rescuing some species that we depend on for our welfare. Many, many example. Perhaps the most significant might be in the case of the rice industry, and the grassy stunt virus. And the, I guess, three individuals from a very peripheral population in India, that is now extinct, retained alleles that conferred resistance on this very damaging disease. That basically rescued the entire rice industry and, actually, the lives of many people throughout Southeast Asia. Again, alleles locked into one isolated population, that evidently no longer exists. But lots of examples of how, from just a perspective of human welfare, how this diversity within species is actually very important.

And last. For conservation biologists are often dealing with these issues in one fashion or another, those with mandates to perhaps establish seed banks that are representative of the entire gene pool of a particular species, or putting together captive breeding programs, I ask these questions quite a bit: How many populations should we be drawing from, or protecting? And this particularly becomes an issue in the context of restoration ecological restoration. Where do we draw individuals from? How many individuals do we need to capture the variation that was originally present? To, you know, reconstitute populations, and sometimes species, into the process of restoration.

Just in terms of the details of interspecific genetic variation how it's distributed we certainly get a lot of new insights that have been accumulating. I think the last 30 years, with allozyme studies, this is the general picture that's begun to be drawn from, again, thousands and thousands of allozyme studies. Just in terms of the polymorphic portion of the genome, again, as represented only by allozymes here, we're talking about 50% in plants, and about 15% in animals. The question then is: How is that distributed across species ranges?

This is a table drawn from John Avise's book in 1994. It nicely summarizes these studies, in terms of how the variation that occurs within species is actually distributed among populations. And you can see, looking down, in terms of different taxonomic groups this is the fraction that is

essentially accounted for by geographical differences. This is the fraction that we stand to lose, basically, if species ranges collapse to too great an extent.

You can see, for example, in the fairly maybe the less-well-dispersing groups mammals, reptiles, amphibians. There's a lot of complicated processes behind these. But you can see a fairly substantial component of the variation that characterizes these species is associated with local population has a geographical component. And this is what we stand to lose, again, when we drop to single populations, or just a few scattered populations, from the original geographic ranges.

As I say, when populations decline, ranges also generally collapse or retreat, correspondingly. Just the dimensions of that issue. This is a very interesting report done by The Nature Conservancy in 1997. Surveyed about 21,000 species, I guess, of plants and animals in the U.S., and found about The good news is, two-thirds of the species are demonstrably secure or apparently secure. The bad news being that a third of all the species in the U.S., in one fashion or another, have declined substantially both populations and ranges and are currently in some state of imperilment or endangerment. And this is just data for the U.S. I expect it's comparable in other parts of the world or maybe even more dire. But this is what we're talking about.

A third of all plants and animals having shown these fairly substantial changes and range contractions. Rather bothersome in some groups. For example, flowering plants are right there with that one-third. But given their overall species diversity, we're talking about some 5,000 species that can be said to have declined substantially. And some groups are extremely overrepresented in this declining fraction. Mainly aquatic organisms mussels, amphibians, fishes and crayfish.

When we think about range contractions we have some fixed notions about how it happens. This is just an example of what we usually visualize. This happens to be the scissor-tailed flycatcher range in the U.S. But because populations on the peripheries of ranges tend to have lower densities tend to be much more variable temporally variable. These are the factors that are, you know, generally associated with lower population viability. Our notion are that these ranges contract toward the core, or the center, of these distributions, to where numbers tend to be higher, and where populations tend to be more stable.

The reality of it is really quite different from that. Only recently have people begun to dig into this. One individual, Mark Lomalino, has compiled, actually, the process in about 300 different species of mostly animals. And, basically, we have it all backwards. For reasons that aren't entirely clear at this point, in a nutshell, species tend to retreat not to their cores, but to their peripheries. These maps are just examples the black being the historical range, and the white being the current, or extant, range of these different species. And they're not doing at all what we expect. They seem to be pushed out to the margins, and that's where they persist and hang on.

And, again, this is occurring in about 70% or some odd of the species that have been examined. And it just brings back to genetics it's not entirely clear. Another thing that we don't really understand. We have this notion that the peripheral populations tend to be genetically depauperate, because of all the turnover and instability. But at least with the plant literature and the drosophila literature, we don't seem to indicate any such pattern. There tend to be comparable levels of genetic diversity at the core or at the periphery.

One thing I would point out is, I guess, what I see as an unfortunate synergy here, in terms of the very factors that promote divergence and diversification within species are the very factors that also seem to predispose taxa to endangerment: poor dispersal abilities; low gene flow; extreme rates of

phylopatry. Basically, you'll see the same groups showing up in the endangered fraction on The Nature Conservancy's species report card that you'll also find displaying the highest levels of genetic divergence within species. So those species that, perhaps, most need to hang on to most of their populations, in order to retain their full genetic complement, are those that are also most vulnerable to range contractions and population declines.

How do we better frame this issue? It's a little complicated. And this is something that I've been wondering about ever since I read Ehrlich's paper some 10 years ago. And partly because I often get the question. It's a fairly direct question; it should have some pretty simple answers. But, essentially: How many populations are we talking about? If we really want to capture all the variation that occurs in a particular species, are we talking about one population? Three? Ten? A hundred? What fraction?

So a question that's asked by people that are setting up networks of protected areas the question is asked by people who are, perhaps, collecting seeds to establish seed banks; or maybe even putting together captive breeding populations of vertebrates in different facilities. But it's a fairly simple question. And, particularly, to put this in a context that people can really relate to: What is, basically, the relationship between the effort expended and the gain sort of received? In terms of: What is the point of diminishing returns, in terms of protecting more populations versus protecting more and more allelic diversity?

Don Falk, who I've been working with for the last year, has written a couple of really interesting papers in which he's basically joined economic models to population genetics, to try and put this in a larger framework. And, basically, in terms of. He sees basic relationships here of a number of populations, from few to many. And what's at stake in terms of as you ratchet down population by population, how much genetic variation you lose. Generally, in this end of the scheme you can be losing populations, because perhaps some of the genetic variation is already present in some of the remaining populations. But as you get to very small numbers, the marginal increment of genetic-variation loss jumps up quite substantially.

This is another way of looking at it. As you protect more and more populations or as you sample from them, and collect from them, for seed banks you're going to be capturing more and more of the genetic variation that characterizes that particular species. And you'll reach some threshold at some point where you've got most of it. Further sampling protection doesn't buy you much.

The first time I saw these patterns, it just jumped right out at me, in terms of: Boy, this curve looks familiar. It looks like a species-area curve; a species-effort curve; a rarefaction curve. Lots of names for these collector's curves, sampling curves, but ecologists use these all the time. For example, in rapid ecological assessments, you'll see these very same patterns. And it's the same problem: How much sampling do we need to do in order to capture most of the diversity that's present? Here we're just talking about alleles, rather than species.

And I got to thinking that: Maybe you could just mine the literature that's already out there, and just put together some. Again, there's thousands of studies of allozymes, in particular, drawn from many different populations across species ranges, and that are quite amenable to an analysis of this kind. So Don had taken it to this theoretical point. And I thought: Give it a try, and see if you could actually approximate some of these curves with actual data.

And all we're talking about doing is going into these published studies and drawing out single populations doubles, triplets, quartets, etc. drawing them at random, and looking, roughly, at how we accumulate alleles with each additional population added. And, lo and behold, the patterns are really quite similar to what

he had drawn. These are two species of phlox from Texas part of Don Levin's classic studies done ... incredibly exhaustive studies. I suppose, in this day, we've heard all about advancing technology, maybe less so. But 70 populations, in the case of this species, with, oh, a good 20 to 30, and even more, individuals per population and a good 20 to 30 alleles surveyed at the same time.

But you're seeing the basic pattern here, of For example, with *Phlox drummondii* here, with a single population, you generally capture about 70% of the overall variation that was detected throughout that species. And when you get to about 10%, you're already hitting sort of an asymptote where further protection or acquisition really would give you some pretty diminishing returns.

*Cuspidata* is another this species is another matter. Even toward 20 or 30 populations, you're still far from reaching any kind of an asymptote here, in terms of capturing most of the variation in that particular species.

*Plethodon cinereus* perhaps the most divergent of all species studied. I'm not sure if that still stands. But you can see, even after This is from Richard Highton's studies of allozymes. Even after, oh, 20 populations, we're a long way from even coming close to any kind of an asymptote here. And particularly when we look at rare alleles alleles that are found nowhere at a frequency greater than 10%. They're very much on the incline here. And we're working on how to legitimately project these toward their true asymptotes, and sort of mathematical models that are most appropriate. Fortunately, ecologists have spent a lot of time thinking about this. We're basically able to co-opt a lot of thinking that ecologists use, and apply it to genetic data.

Just two more sets of these curves, and I'll bring it to a conclusion. But we've started to march through studies, and being kind of choosy about the studies. They need to have involved lots of individuals, drawn from lots of populations across species ranges and you do see some very intriguing patterns, with, just called perhaps the quick saturators. These are plants that, with relative few populations, you're reaching a saturation point reaching the asymptote. There's really not much more to be collected, or protected, with more than, say ... more than 10 populations.

Slow saturators are another matter entirely. These are, again, species quite a mix here. Some of these endangered, some of them quite common. But even with substantial sampling here, we're very much, still, on the incline, and we're looking at not reaching a point of diminishing returns for quite some time.

One could ask: What does this tell us that F statistics don't already? And I tend to agree. These do broadly mimic the basic patterns you'd find with F statistics. But what they do is, I think they put them in a framework that's much more accessible to managers and policy-makers, in terms of they want to know specific population numbers; returns in terms of on effort and investment. And that's really what these curves show.

Assumptions there are quite a few. We're dealing with published genetic data, and we assume they represent a random sampling of alleles, individuals and populations from within species ranges. We are pretty picky about the studies we include, but I'm sure there are some violations quite a few, in fact. But we assume that the original studies detected all alleles in each population. Many of them We don't use any study that has sampled less than 10 individuals per population but, still, that's probably inadequate. It certainly is to detect all the alleles present.

And last, of course, does enzyme variation measured by electrophoretic methods actually index the entire genome, if we're trying to draw general inferences about patterns in genetic diversity in these species? Whatever the case, I think the method is incredibly flexible. You can apply this to any class of

genetic markers. You can even apply it to morphological variants if you have the data and it's so quantified. I think this will only apply within the context of the markers you're concerned with, but it does have some flexibility.

So, just to conclude clearly, when we see population declines in species range contractions; as we lose populations, we're going to lose some part of the component, that population component of variation that occurs within species. The extent to which that occurs depends a lot on the genetic structure of the species and the populations within it. I tried to outline a fairly simple and intuitive and, perhaps, flexible method here for better communicating what's at stake here.

And I think the terms of these marginal diversity functions and cumulative diversity functions these are the sorts of contexts that managers have to think in every day. And I hope that this takes us somewhat closer to bridging what is a fairly substantial gap between theory and application in conservation biology and conservation genetics.

So I will end there, and thank you.

(Applause)