

DIVERSITY, STABILITY, AND ECOSYSTEM FUNCTION

Introduction

We're at that point in the course where we're switching gears. We've spent the last six weeks focusing on the biology of small populations: an overview of the U.S. Endangered Species Act and how it is used to manage and protect species that are recognized as threatened or endangered by the federal government, understanding the deterministic and stochastic threats to persistence, integrating our understanding of those threats into analyses of population viability, and applying that understanding to several well-studied examples of threatened populations—the black-footed ferret, the northern spotted owl, the bay checkerspot butterfly, and the black sea turtle. For the next five weeks we're going to be talking about conservation biology as it applies to more than one species at a time. We'll be talking, for example, about the cumulative effects of species loss on ecological communities and about principles of conservation reserve design.

We'll start by examining the widespread belief that the more diverse an ecosystem is, the more stable it will be. I should point out right now that even though I'll be raising some substantial doubts about simple formulations of this belief and how useful it is for conservation purposes, it's not an unreasonable notion. It was, after all, first formalized by none other than Robert MacArthur in a very influential paper in *Ecology* [10]. Before we can talk about this relationship, however, we need to decide just what *diversity* really is.

Whittaker [17] distinguished three types of diversity.

1. *alpha* diversity — diversity within a particular area or ecosystem
2. *beta* diversity — the change in diversity between ecosystems
3. *gamma* diversity — the overall diversity in a landscape comprised of several ecosystems

For me an analogy from population genetics helps clarify the point.¹ Rosenberg et al. [13] studied microsatellite variation in human beings at several hundred loci. They were able to

¹Of course, I'm a population geneticist, so this way of thinking about the world comes naturally to me. If it doesn't come naturally to you and you don't find this analogy useful, feel free to ignore it.

distinguish five major geographical groupings of populations: Africa, Eurasia, East Asia, America, and Oceania. Of the total diversity in human populations, roughly 10% of the diversity is a result of differences among the different geographical groupings. Diversity within each geographical grouping corresponds to alpha diversity, the total diversity within human beings corresponds to gamma diversity, and the proportion of diversity due to differences among geographical populations (10%) corresponds to beta diversity.

Most analyses for conservation purposes have focused *only* on species diversity—attempting to identify regions with a large number of species. You all probably realize, however, that there are several aspects to diversity:

- Number of different species
- Relative abundance of different species
- Ecological distinctiveness of different species, e.g., functional differentiation
- Evolutionary distinctiveness of different species

We also won't discuss formal definitions of ecological diversity,² which are primarily definitions of alpha diversity although they can be generalized to allow partitioning of gamma diversity into its alpha and beta components.³ These definitions treat all species as equivalent, ignoring aspects of ecological and evolutionary distinctiveness. Until relatively recently, many experimental evaluations of the diversity-stability hypothesis did the same.

Diversity and Stability

Over the past few decades, it has been commonplace for conservationists to appeal to the *diversity-stability* hypothesis as a component of their arguments for the importance of conserving biological diversity, at least in popular writings. Consider, for example, the following passage from Barry Commoner's book, *The Closing Circle*:⁴

The amount of stress which an ecosystem can absorb before it is driven to collapse is also a result of its various interconnections and their relative speeds of response. The 'more complex the ecosystem, the more successfully it can resist a stress . . . Like a net, in which each knot is connected to others by several

²You can find a brief survey of them in the Appendix if you're interested.

³If you happen to have run across F -statistics in population genetics, you know what I'm referring to. If you haven't, don't worry about it.

⁴This section draws heavily from [11, pp. 73–89].

strands, such a fabric can resist collapse better than a simple, unbranched circle of threads – which if cut anywhere breaks down as a whole. Environmental pollution is often a sign that ecological links have been cut and that the ecosystem has been artificially simplified [3]

Principles

Robert MacArthur [10] proposed measuring the stability of an ecosystem by measuring the number of alternative pathways it contains through which energy can flow. He justified this measure by arguing that an ecosystem with many pathways, representing an abundance of species organized in a complex food web, tends to equilibrate fluctuations in population as predators will switch from less abundant to more abundant prey species, lowering population densities of the more common and allowing the density of the less common to increase.

Charles Elton [5, pp. 146–150] gave six reasons for thinking the hypothesis to be true:

1. Evidence from mathematical models suggests that those with few species are inherently unstable.
2. Laboratory experiments are consistent with the mathematical models.
3. Habitats on small islands are more susceptible to invasion than are those on continents.
4. Less diverse habitats of cultivated or planted land are more susceptible to invasion than undisturbed habitat.
5. Highly diverse tropical forest ecosystems are relatively resistant to pest invasion.
6. Orchard spraying, which simplifies ecological relationships, tends to increase the likelihood of severe oscillations in pest populations.

In 1975, Daniel Goodman summarized the mounting evidence against the diversity-stability hypothesis by responding to each of Elton’s arguments for it [6]

- 1,2 Models of more complex communities showed just the opposite of what Elton asserted. The more species that interact the less likely the system is to be stable.
- 3 The data suggesting vulnerability of islands to invasions by pest species may result from accidents of distribution or other special characteristics of islands.⁵

⁵I don’t find this argument particularly convincing. The biotas of temperate (e.g., Juan Fernandez, New Zealand), subtropical (e.g., Canary) and tropical (e.g., Hawaii) islands have all been dramatically altered through species introductions. It is, however, difficult to be certain that this is because island communities are more “open.” It could reflect habitat alterations that make them more suitable for aliens than natives.

4,6 Crops and orchard tree planted in pure stands do not represent equilibrium low diversity systems. It is difficult to find evidence that naturally low diversity communities are more susceptible to invasion than naturally high diversity communities.⁶

5 The tropical biota is so diverse and complex that large fluctuations might go unnoticed. Furthermore, there is evidence that even highly diverse systems can be dramatically altered by invaders, e.g., the impact of the crown-of-thorns starfish on coral reefs.

Empirical results

Tilman and Downing [15] suggest that primary productivity in more diverse plant communities is more resistant to, and recovers more fully from, a major drought.

- 207 plots of prairie grasslands differing in species richness from 1 to 26.
- Measured resistance as relative rate of community biomass change from 1986, the year before a drought, to 1988, the peak of the drought.
- Drought resistance is an increasing function of community diversity.
- Saturates at about 10–15 species.
- More diverse communities are more resistant⁷ than less diverse communities, but they don't have to be very diverse.
- Recent results on the relationship between bacterial species diversity and community respiration (a measure of total microbial activity) show that there are diminishing returns as the number of species in the bacterial community increases [1]. The strong diminishing returns associated with increases in species diversity are likely to be a general feature of relationships between ecosystem processes and species richness.

In a similar experiment Tilman et al. [14] found that plant cover is an increasing function of species richness and lower concentrations of inorganic soil nitrogen, presumably because of greater nitrogen uptake in more diverse communities.

Experiments on mycorrhizal diversity [16] suggest that plant species composition and community structure are more sensitive to the present or absence of particular mycorrhizal

⁶Again, it is difficult to be certain the low diversity of agricultural systems causes their susceptibility to invasion by exotics. Changes in the biotic and abiotic environment associated with agriculture might simply make it a more suitable habitat for new introductions than native species.

⁷Is this the same as stable?

associates when the diversity of mycorrhizal fungi is low. Similarly, plant species diversity, nutrient capture, and productivity are increasing functions of mycorrhizal diversity.

But there are two possible explanations for patterns like these:

1. More diverse communities could increase the chances that at least one species within them is highly productive – a *selection* effect.
2. More diverse communities may be able to tap resources more effectively because they differ in strategies for resource acquisition – a *complementarity* effect.

Cardinale et al. [2] perform a meta-analysis of 111 field, greenhouse, and laboratory studies that manipulated species diversity to determine its effect on abundance and biomass. They found that

- Decreasing diversity is, on average, associated with decreased abundance, decreased biomass, or both.
- The standing biomass of the richest polyculture tends to be no different from that of the most productive monoculture.

“Collectively [their] analyses suggest that the average species loss does indeed affect the functioning of a wide variety of organisms and ecosystems, but the magnitude of these effects is ultimately determined by the identity of species that are going extinct” [2, p. 989]. Using a somewhat different approach Grace et al. reach a similar conclusion: “[T]he influence of small-scale diversity on productivity in natural systems is a weak force, both in absolute terms and relative to the effects of other controls on productivity” [7, p. 680]

More recently Raymundo et al. [12] present evidence that when coral reefs are associated with diverse fish populations, the coral are less susceptible to disease. In looking more closely at their data they found that the abundance of chaetodontid butterflyfishes was positively associated with the extent of disease. Butterflyfishes were more abundant in less diverse communities because they are released from competition – a selection effect in the opposite direction from what we would normally think of.

Functional diversity

Diaz and Cabido [4] point out that experiments like those just described focus only on the *number* of species present, not on the *functions* they play in an ecosystem. They summarize evidence from a variety of studies suggesting that ecosystem processes depend on *functional* diversity far more strongly than on species diversity *per se*. They suggest two plausible explanations:

1. *Functional redundancy*: Two or more species in a particular ecosystem may play essentially the same role in ecosystem processes. It may, for example, make relatively little difference to the nitrogen dynamics which particular species of legumes are present, only that there are some nitrogen-fixing plants present. The loss of species with similar functional effects⁸ should have relatively little effect on ecosystem processes.
2. *Functional insurance*: The more divergent species in an ecosystem are with respect to their influence on ecosystem processes, the smaller the number required to buffer an ecosystem against change. Species with similar functional effects that differ in functional response⁹ may buffer ecosystems against externally imposed change because the species that influence each ecosystem response may respond differently.

Concepts of diversity and stability

Part of the problem here is that it's not entirely clear what we *mean* by stability, nor what aspect of diversity we are considering.

- Are we concerned only with the number of species in the community and its relation to stability, or are we concerned with how evenness relates to stability, or are we concerned with some combination of both? Work I am aware of that considers the problem focuses only on species diversity, i.e., the *number* of species present, and only recently has begun to consider the the degree of functional diversity represented.
 - In one sense this may be legitimate. After all, part of the reason conservationists have invoked the diversity-stability hypothesis is to justify concern about the loss of individual species.
 - We may also be missing something important. If other aspects of diversity play an important role in the structure and function of ecosystems, a focus on the *number* of species alone may blind us to the role that evenness plays in the ability of ecosystems to respond to changes in energy and nutrient inputs.
- There are at least three ways in which stability might be defined.
 1. *Constancy*—The ability of a community to resist changes in composition and abundance in response to disturbance. Not a particularly useful concept of stability for conservationists because

⁸*functional effect*: the effects that a species has on some aspect of ecosystem function.

⁹*functional response*: the way in which a species responds to changes in the ecosystem.

- Few, if any, ecosystems could be described as constant.
 - Even those that have powerful mechanisms for reacting to environmental fluctuations do so through internal changes that return the system as quickly as possible to a stable state. But these involve responses and changes. It seems better to regard them as examples of *resiliency* than of constancy.
2. *Resiliency*—The ability of a community to return to its pre-disturbance characteristics after changes induced by a disturbance. Resiliency corresponds to stability the way it is studied in mathematical models. Are deviations from an equilibrium reduced with time (stable) or amplified with time (unstable)? Still, it has little applicability to actual ecosystems. It measures a system’s tendency to return to a single stable point, but
- Many ecological systems appear to have multiple stable points. If disturbance remains below a particular threshold, it will return to its predisturbance configuration. If it exceeds that threshold, it may move to a new configuration.
 - Furthermore, most ecological systems change not only in response to disturbance but also in response to natural, successional change.
 - There is little evidence that ecological communities *ever* represent an equilibrium configuration from which it would make sense to study perturbations.

Constancy and resiliency have this in common: both focus on species persistence and abundance as measures of stability.

3. *Dynamic stability*—A system is dynamically stable if its future states are determined largely by its own current state, with little or no reference to outside influences. In many ways this seems to correspond with our intuitive notions of stability and to make sense of the relationship between diversity and stability.
- Recall the quote from Commoner: “The more complex the ecosystem, the more successfully it can resist a stress.”
 - A system that is dynamically stable is one that is relatively immune to disturbance. A rapidly spinning gyroscope is dynamically stable because the gyroscopic forces that it generates resist external forces that would alter its plane of rotation.
 - It reflects our hope that stable systems should be able to maintain themselves without human intervention.
 - A diverse biological system is more likely to be dynamically stable than one that is not diverse because in diverse communities biotic interactions may often play a larger role in a species’ success than its interactions with the

physical environment. To the extent that changes in the system are driven by biotic interactions, it is dynamically stable, since characteristics of the system itself are determining its future state.

There are some problems with this formulation of the diversity-stability hypothesis, however.

- Although the last thing I said *sounds* plausible enough, it constituted only a little more than proof by vigorous assertion. How can we identify systems whose future state depends primarily on their own internal characteristics? Are there any?¹⁰
 - If we don't know how to identify systems that are dynamically stable, we can't even test the diversity-stability hypothesis to see if it's true.
 - It verges on circularity. The larger (more diverse) the system considered, the fewer are the things left out of it. The fewer the things left out, the smaller the possible outside influences on the system. The smaller the possible outside influences, the greater the degree of dynamic stability. Thus, dynamic stability is (almost) a necessary consequence of diversity, simply because diverse systems include many components.¹¹
 - Moreover, the argument as presented says nothing about the *types* of diversity present, e.g., a diverse community assembled from non-native species would fill the bill just as easily as one composed solely of natives.
- Ives and Carpenter [9] suggest a different approach to understanding community stability (Figure 1).
 - Alternative stable states
 - Non-point attractors
 - Pulse perturbations
 - Press perturbations
 - Extinctions
 - Invasions

¹⁰Even the earth's ecosystem taken as a single unit doesn't satisfy this definition. It depends critically on continual energy input from the sun. Perhaps the way to say it is that there is no *variation* in relevant external inputs to the system.

¹¹It's not entirely circular because, as the example of the gyroscope makes clear, it's also possible for simple systems to be dynamically stable.

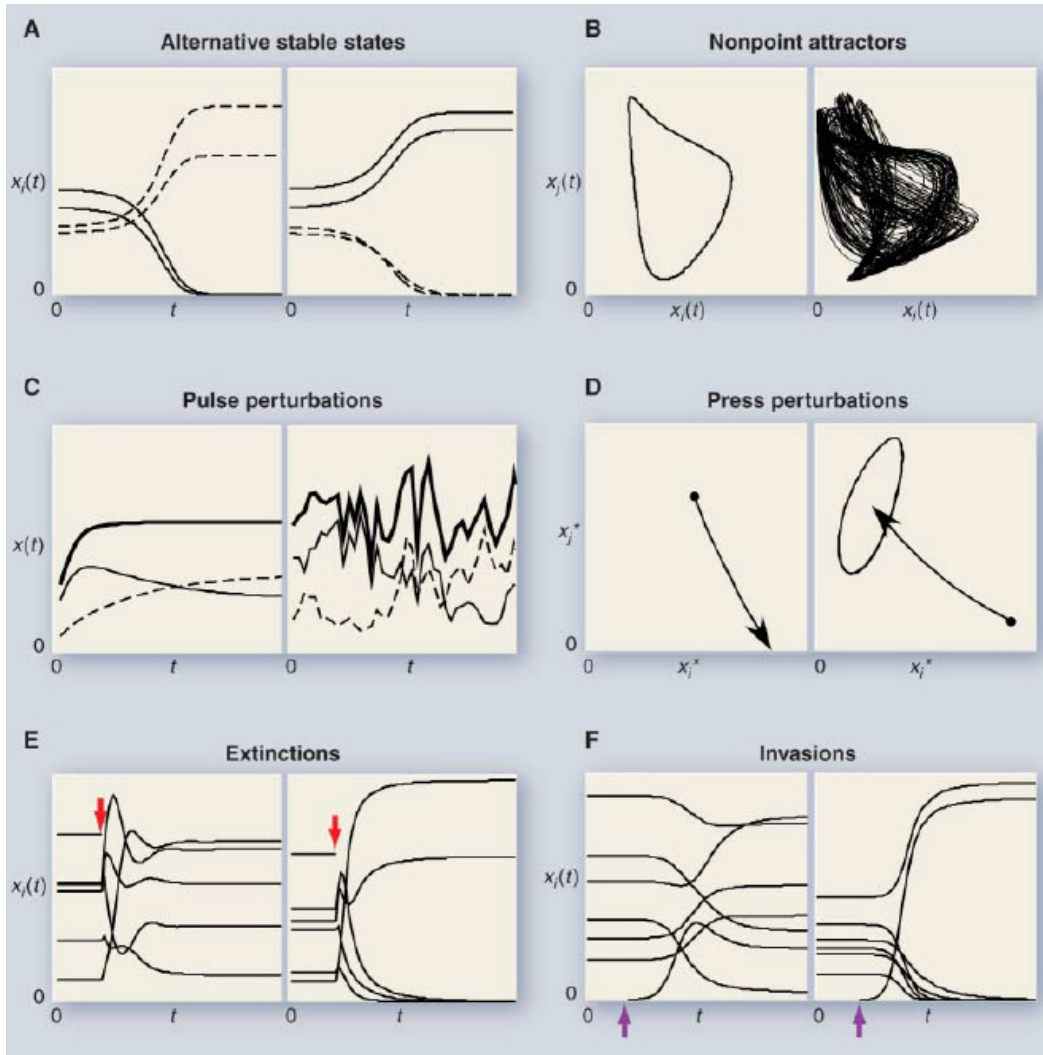


Figure 1: Types of stability, perturbations, and community responses. From Ives and Carpenter [9].

Their approach strikes me as quite useful, first because it emphasizes that systems move to a region different from the one from which they were perturbed¹² and second because it reminds us that things other than diversity, like the frequency and character of perturbation, may affect the stability of ecosystems.

- Biological integrity — “Biological integrity refers to a system’s wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates.”¹³
 1. What are “appropriate elements”?
 2. What are “appropriate rates” of processes?

“By definition naturally evolved assemblages possess integrity but random assemblages do not.” Therefore, provides justification for management focusing on *native* species rather than introduced ones.

This seems like the logical fallacy of *affirming the consequent*, but

- Species composition of lakes exposed to nutrient enrichment or acidification responds more quickly and recovers more slowly than processes like primary production, respiration, and nutrient cycling.
- Shifts in biotic composition don’t necessarily lead to changes in process rates.
- Angermeier and Karr suggest that these observations means a focus on integrity rather than diversity makes sense. To me it makes more sense to conclude that species changes are a more sensitive indicator of what’s going on than process changes.
- Loss of native species from a system is truly “a canary in the mine,” a warning of process changes that may have consequences much larger than we suspect.

Conclusions

Naive versions of the diversity-stability hypothesis probably aren’t true and do not provide a solid conceptual basis for arguing that conservation of biological diversity is an important goal. A less specific version, one that defines stability as a dynamic property related to

¹²We’ll see a good example of this when we talk about changes associated with some plant invasions later in the course.

¹³Angermeier and Karr, *BioScience* 44:690–697; 1994

the degree that the components of a system determine their own future state, provides a plausible basis for the hypothesis. Unfortunately, this version of the hypothesis verges on circularity and is almost immune to empirical investigation. Moreover, a system that is “stable” with respect to some perturbations — hurricanes, drought, or other extreme weather events — may not be stable to others — invasion by exotic plants or animals, extinctions of component species, or other biotic changes. As far as practical conservation applications are concerned, it is not obvious to me that the diversity-stability hypothesis provides anything more than a useful heuristic.

There is something to the idea of biological integrity. Changes in species composition and community structure may alert us to underlying changes in ecosystem processes more quickly than direct attempts to measure these processes. Diverse systems provide more indicators of change in these underlying processes and if we can manage the systems so that they are protected, then the underlying processes will remain intact, too.

Chapin et al. [8] summarize it this way:

- High species richness maximizes resource acquisition at each trophic level and the retention of resources in the ecosystem.
- High species diversity reduces the risk of large changes in ecosystem processes in response to directional or stochastic variation in the environment.
- High species diversity reduces the probability of large changes in ecosystem processes in response to invasions of pathogens and other species.
- Landscape heterogeneity most strongly influences those processes or organisms that depend on multiple patch types and are controlled by a flow of organisms, water, air, or disturbance among patches.

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Appendix: Measures of diversity

How do these results compare with standard indices of diversity? Patil and Taillie¹⁴ note that in a diverse community, the typical species is rare. They suggest defining diversity as the *average rarity of species within a community*.¹⁵

How do we formalize this?

$$\text{Community} = C = \{s; \pi_1, \pi_2, \dots, \pi_s\} \quad ,$$

where π_i is the proportion of all individuals that are of species i , and s is the total number of species.

$$\pi_i = \frac{N_i}{\sum_{k=1}^s N_k} \quad .$$

Let $R(\pi_i)$ be our measure of rarity for a species with a particular frequency of occurrence. Then the average rarity of species in the community is:

$$\Delta(C) = \sum_{k=1}^s \pi_k R(\pi_k) \quad .$$

A common species has a large π_k (close to 1) and a small $R(\pi_k)$ (because we are not surprised to find it). Conversely, a rare species has a small π_k , and a large $R(\pi_k)$.

Simpson’s diversity index

Suppose $R(\pi_k) = 1 - \pi_k$, the probability that the next species you encounter is *different* from the one you have just seen. Then

¹⁴Patil, G. P., and C. Taillie. 1979. An overview of diversity. In *Ecological diversity in theory and practice*, ed. J. F. Grassle, G. P. Patil, W. K. Smith, and C. Taillie, pp. 3–27. Intl. Co-operative Publ. House, Fairland, MD.

¹⁵Note: this approach does *not* take account of either ecological or evolutionary distinctiveness.

$$\begin{aligned}\Delta_1(C) &= \sum_{k=1}^s \pi_k (1 - \pi_k) \\ &= 1 - \sum_{k=1}^s \pi_k^2\end{aligned}$$

For those of you who've had population genetics, you can think of the π_k as allele frequencies and Simpson's diversity as the panmictic heterozygosity. It's the probability that any two individuals chosen at random from the community belong to different species.

Species richness

Suppose on the other hand that $R(\pi_k) = \frac{1-\pi_k}{\pi_k}$, the probability that the next species you encounter is different from the one you have just seen *relative* to the probability of encountering the same species again. Then

$$\begin{aligned}\Delta_{-1}(C) &= \sum_{k=1}^s \pi_k \left(\frac{1 - \pi_k}{\pi_k} \right) \\ &= s - 1\end{aligned}$$

We subtract one from the number of species since a community with only one species has zero diversity.

Shannon diversity index

Suppose that $R(\pi_k) = -\ln(\pi_k)$. This corresponds, roughly, to saying that a species that is rarely encountered is almost infinitely rare while a species that is commonly encountered is not rare at all. This might be appropriate if we think of $R(\pi_k)$ as measuring how much value we place on a species as a function of its frequency of occurrence in a community. Then

$$\begin{aligned}\Delta_0(C) &= \sum_{k=1}^s \pi_k [-\ln(\pi_k)] \\ &= -\sum_{k=1}^s \pi_k \ln(\pi_k)\end{aligned}$$

Patil & Tailie

Both Simpson's index and Shannon's index are affected by the number of species and the evenness of species abundances, but they are affected differently. A rare species contributes much less to diversity in Simpson's index than in Shannon's. Patil & Tailie point out that all of these diversity measures can be subsumed in a single diversity spectrum. Let $R(\pi_k) = \frac{1-\pi_k^\beta}{\beta}$. β scales the relative importance of richness and evenness. Then

$$\Delta_\beta(C) = \sum_{k=1}^s \pi_k \left(\frac{1 - \pi_k^\beta}{\beta} \right) .$$

A little algebra (and l'Hopitals rule from calculus) shows that

$$\begin{aligned} \text{if } \beta = -1, \Delta_\beta &= \text{species richness} \\ \text{if } \beta = 0, \Delta_\beta &= \text{Shannon's index} \\ \text{if } \beta = 1, \Delta_\beta &= \text{Simpson's index} \end{aligned}$$

Thus, "diversity profiles" can be plotted to compare two or more communities over a range of evenness emphasis from no emphasis at all (species richness) to high emphasis (Simpson's index).

Notice that *all* of these measure treat species as if they were completely interchangeable with one another. A community in which there were 100 species of sedges, and nothing else, all in equal frequency would receive the same diversity score as one in which there were 10 species of sedges, 10 species of grasses, 10 species of legumes, 10 species of roses, 10 species of buttercups, and 50 species of composites, all in equal frequency. How do we feel about that?

Again the tyranny of numbers. Don't forget why we started calculating these things in the first place. They are a guide, not a formula, and you shouldn't hesitate to trust your gut instincts if the formula seems to be giving you the wrong answer. If it *does* conflict with your gut, however, you'd be well-advised to figure out *why*. Identify what's wrong with the formula, what it's leaving out that's important, how it measures the wrong thing, etc.

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