Does Ecosystem Stability Depend on Biodiversity?

By
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Abstract:

Biodiversity is considered to be an important factor in the maintenance of stability of biological systems. Higher biodiversity leads to a more stable ecosystem. However, there are contradictory opinions on the subject.
Different factors may lead to stability loss. The very same factors almost always also cause loss of species diversity. Loss of ecosystem stability seems to be related to loss of biodiversity. For restoration of ecosystem stability the ability of re-introduction of species is needed. And to prevent the los of stability, resilience may be improved by increasing genetic diversity of species. Considering that higher biodiversity is better for stability the possibility of non-native species to increase ecosystem stability needs to be explored.

Introduction:

There has been considerable discussion about the suggested value of biodiversity (McCann 2000). Biodiversity is considered by some to be an important factor in the maintenance of stability of biological systems. In this revue I examine the evidence that the stability of biological systems can be affected by diversity and the proposed mechanisms by which they work.
Understanding what contributes to stability is necessary to adopt measures to preserve valuable ecosystem functions in a changing environment and if necessary, be restored.

Ecosystem stability
A community is generally considered stable when the abundance of species stays relatively constant, and unstable when the abundance has strong fluctuations (MacArthur 1955). In addition we will also consider a community more stable if large changes has little effect on other species. In general, stability increases as population densities move away from very low or high extremes (McCann 2000).
An important part of ecosystem stability is its ability to absorb disturbances and to quickly return to similar functions after being disturbed. This ability is called resilience(Folke et al. 2010).
An unstable ecosystem is very reactive to changes and may change unpredictable and sudden (Lehman & David Tilman 2000). An unstable ecosystem may for example be vulnerable to invasion of exotic species together with removal of native species(Fargione & David Tilman 2005).
And such instability can cause a cascading effect where the loss of one species results in changes further down the food-web. This change would then lead to other species not being able to cope within that environment, making it even more vulnerable to more change. This vulnerability in its turn would then possibly lead to even more los of

species (Petchey et al. 2008). An example of such a cascade effect was seen with the decline in whales leading to killer whales to pray more on other species causing the loss of sea otter (see figure 1) which led to an ecosystem shift (Springer et al. 2003).

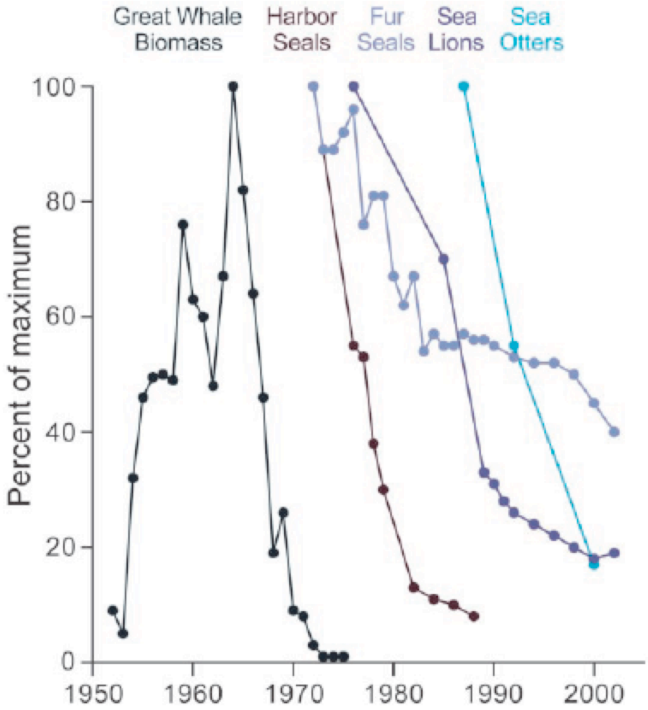

Figure 1: The sequential collapse of marine mammals in the North Pacific Ocean and southern Bering Sea, all shown as proportions of annual maxima. Great whales: landings (in bio- mass) within 370km of the Aleutian archipelago and coast of the western Gulf of Alaska. Harbor seals: counts and modeled estimate (1972). Fur seals: average pup production, Steller sea lions: estimated abundance of the Alaska western stock. Sea otters: counts of Aleutian Islands. For fur seals and harbor seals, 100% represents population sizes at the time effects of excessive harvesting ended and "unexplained" declines began (Springer et al. 2003).

If we want to explain ecosystem stability and its importance, we need to consider how the species in the system affect it.

A number of different experiments show that ecosystem stability is positively correlated with biodiversity. This is seen for instance, in a removal experiment in forest fields where removal of different species of plants led to changes to the species composition and a slower return to function (restoration) the more species were removed (Allen & Forman 1976). And in grassland experiments where plots with more plant species diversity are more resistant to drought (D Tilman & Downing 1994).

Of course, because loss of stability can result in loss of species making it difficult to see if the correlation between biodiversity and ecosystem stability is caused because less stable ecosystems have more trouble supporting a large variety of species or because low diverse ecosystems are less stable.

We may consider biodiversity as a leading factor of causing ecosystem stability (equilibrium) and try to explain why biodiversity is important to stability and what type of outside factors influences it.

Biodiversity providing system stability:

Species richness.
The assumption, that biodiversity causes an ecosystem to be more stabile, is called the diversity-stability hypothesis. It has also been called the 'insurance hypothesis'. That is because abundance of species would insure against unexpected change to the ecosystem. The insurance hypothesis states that a community has higher stability at higher species richness. The idea is that different species will respond differently to changes in the environment. This allows species that have similar ecological functions to compensate each other if their contributions change due to environmental change. Thus, greater species richness leads to a decreased variability in ecosystem processes(Yachi & Loreau 1999; T. Bouvier et al. 2012).
Of course, if it were just about the amount of species, the introduction of exotic species would advantage to the system. However, also interactions between species and not just the amounts of species are likely to matter in the stability of the ecosystem.

Species Interactions.
Weak species interactions allow al these species to create a stable food-webs. Weak interactions between species mean that if one species (e.g. a predator) increases in population, the species with which it has a weak interaction does not undergo much effect as a response(Post et al. 2000). This allows the species that are lesser competitors to coexist with species that are better competitors, if the lesser competitor has a weaker interaction with predators.
Predators keep the populations of the species with which they have strong interactions (in other words, have a preference for) down. This gives room for species that compete with those, but if the population density of the preferred species is low and the others are high it can still give the predator a different option(McCann 2000; Post et al. 2000). A good example may be a simplified ecosystem where mice are better competitors for grain than hamsters and where cats prefer mice to hamsters. If there are lots of cats, they will keep the population of mice down by hunting them more, allowing hamsters to be able to compete with mice for grain. If then, there is some disturbance, causing there to be less mice, then the amounts of hamsters will increase because they have less competition for grain. The increased availability of hamsters would affect the behavior of the cats. They will start praying more on the hamsters, giving mice a chance to recover (see figure 2).
So stability should be dependent on how each species fits in the food web. If a new species has a strong competitive advantage for resources and low interaction with predators it will likely exclude others lowering diversity.
Also the variance of response is important. If there is more variance in the response of the species in a community, then less species richness might be required as a buffer for the system (Yachi & Loreau 1999). If species in an ecosystem are lost, shifts occur in the interactions between remaining species. A decrease or complete loss of a prey species forces predators to change in foraging, thus creating more pressure on remaining species.
Conversely, when prey species are without predators, the ones with less competitive advantage will become more vulnerable. With less species that carry curtain functions there is less of a buffer when disturbances make it difficult for some species to perform.

These types of changes reduce the resilience of the ecosystem and make it more vulnerable to disturbances.
For example, if we take our fictional food web (cat, mice, hamsters, …), again but now assume a disturbance big enough to remove the mice completely, the cats would be forced to change their diet. They would now only feed on the hamsters, causing less grain to be eaten. This then, would result in a grain population explosion that would displace other plant species. Eventually, this predation may even lower the hamster population to such a level that it would even lead to cat starvation (see figure 3).

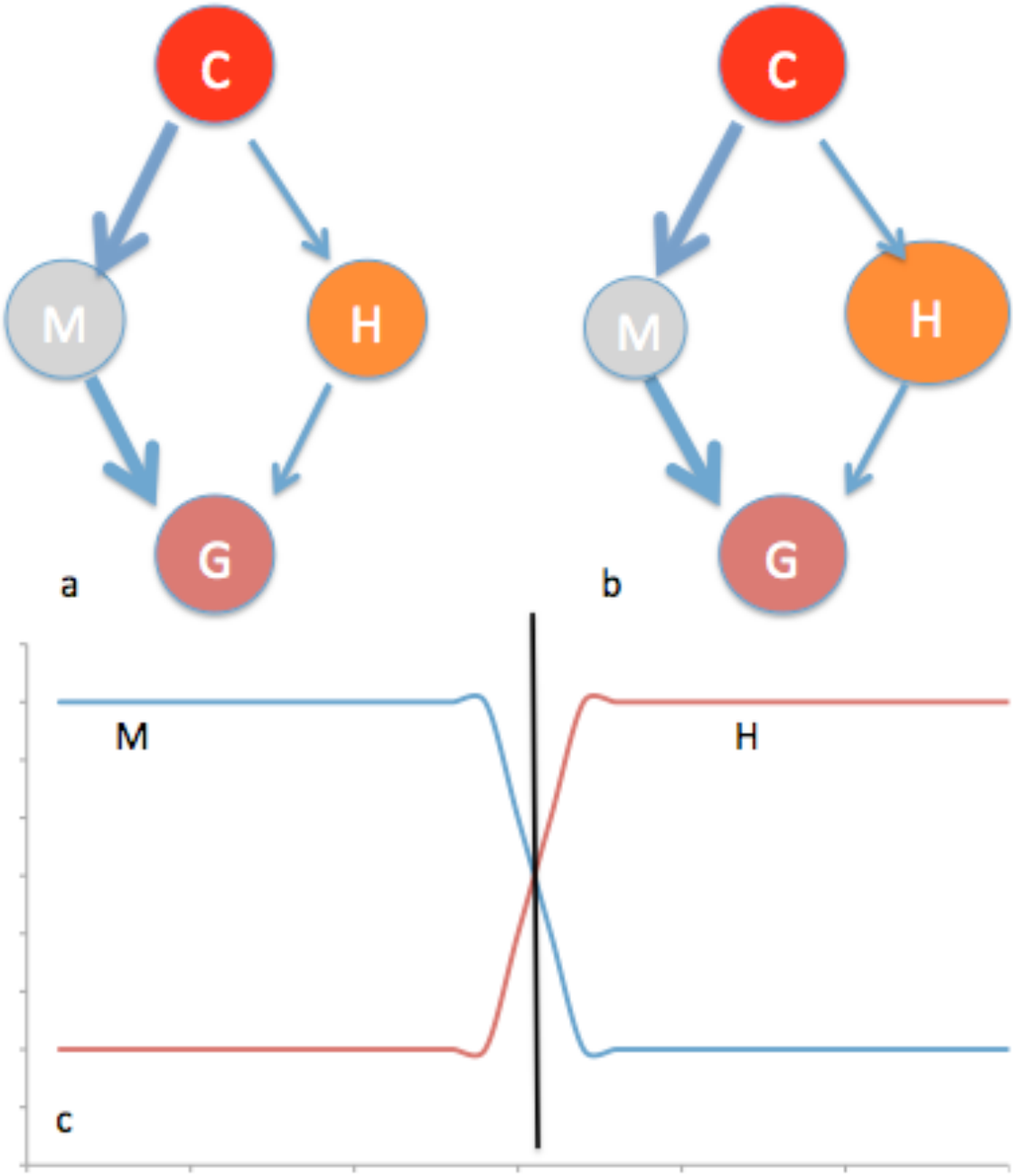

Figure 2: A) A simple food-web diagram depicting strong interactions between cat (C) and mouse (M) and mouse and grain (G) and weak interactions between cat and hamster (H) and hamster and grain. B) A diagram of the same food-web as [A] after a disturbance lowered mice populations leading to a rise in hamsters population shown with the circle size. C) The consumption rates of Hamsters (red) and mice (blue) before and after the disturbance.

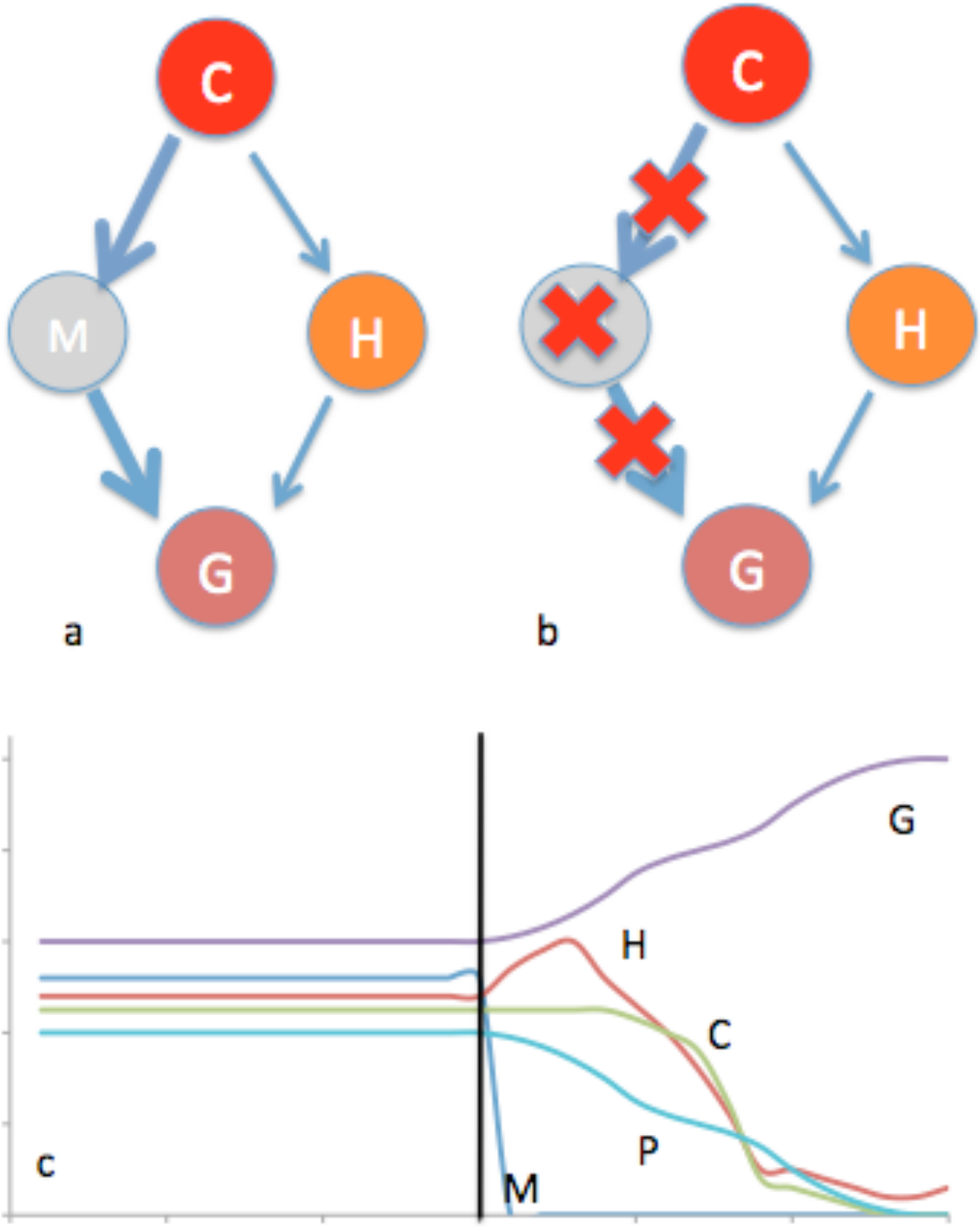

Figure 3 A) A simple food-web diagram depicting strong interactions between cat (C) and mouse (M) and mouse and grain (G) and weak interactions between cat and hamster (H) and hamster and grain. B) A diagram of the same food-web as [A] after a disturbance removed mice populations. C) The population levels of Hamsters (red) and Cats (Green) Grain (purple) and other plants (P, turquoise) before and after the extinction of mice (blue).

Insurance experiments

The insurance hypothesis is also supported by experimental data.

Bouvier et al kept different species of bacterioplankton from two lagoons were kept at different amounts of species diversity. Periodically, disturbances to their environment were introduced by exposing them to different salt concentrations. They observed two effects of diversity when the bacterial communities were confronted with those

disturbances. The first effect was characterized by an increase in temporal mean bacterioplankton abundance and production. Secondly, they observed a buffering effect characterized by a reduction in the temporal variance of production. Here, the higher diversity populations were shown to undergo less disturbance overtime, than the ones with lower diversity. The results highlight the importance of diversity in natural communities as an insurance against environmental fluctuations (T. Bouvier et al. 2012). Tilman et al did grasslands experiment, where various plots were seeded with different amounts of species, the diversity of the plant species increased the stability of the plant production and it decreased the amount of invasive species within the community (David Tilman et al. 2006). This could be explained as an effect of the resource consumption of different layers and time of the diverse species within that community leaving less for invading species to use. Because diverse plots are more likely to contain species that acquire resources at different times and from different depths, they may exhibit more complete resource capture, leaving less resource left over for invaders. (Fargione & David Tilman 2005).

There is also evidence that the insurance hypothesis is true within species. Genetic diversity increases stability because, the more diverse the species, the better it may cope with variations in the environment. Boles et al showed that the bacteria *Pseudomonas aeruginosa* that underwent extensive genetic diversification within biofilm communities. The diversification led to a significantly stronger resistance to environmental stress (Boles et al. 2004).

In conclusion, there seems to be convincing evidence that system stability profits from diversity.

Yet, there is an example where low biodiversity environments showed more stability then ones with high biodiversity (Pfisterer & Schmid 2002). In a grassland experiment where plots of different levels of plant diversity were exposed to drought as an environmental disturbance surprisingly, the low diversity systems showed better resilience.

The species in the low biodiverse environment were also present in the high biodiverse environment. Only the high diversity environments also contained other plants. Therefore the difference in reaction to the disturbance cannot be explained as the species of low biodiverse groups having more variable responses to change.

The observed inverse association between diversity and stability may be due to niche complementarity. The central idea of niche complementarity is that a community of species whose niches complement one another is more efficient in its use of resources than an equivalent set of monocultures. According to Pfisterer and Schmid, this could be its downfall in a diverse system when faced with perturbation (Pfisterer & Schmid 2002). Niche complementarity is disrupted and so the whole community suffers. But this is not so much a problem for less diverse plots.

Another reason could be that the species that becomes the most abundant and productive in a system developed without disturbances are most adapted to that specific environment. The species most adapted to an environment would consequently suffer most from changes in that environment. Thus, if species-rich systems have a greater chance of including species growing well under unperturbed conditions, they may also have a greater chance of loosing this growth potential under perturbation if the two are negatively correlated. (Pfisterer & Schmid 2002).

It seems therefore, that in while in most cases higher biodiversity leads to a more stable ecosystem there is considerable room for discussion (Naeem 2002).

Stability loss
Different factors can be involved in the loss of stability.
Loss of stability can be caused by the introduction of exotic species. The introduction of the Nile perch in Lake Victoria for instance, caused a massive loss of native species within that lake. That event cascaded down to a big change in the total habitat, because some of the native species that fed on the algae were decimated. This facilitated a large growth of algae, which then led to oxygen depletion(Goldschmidt et al. 1993). The introduction of the Nile perch also had its effects outside of the lake. The drying processes for the Nile perch requires more wood than needed for other fish. This has led to a change in the landscape from forests to savannah-like grasslands with very few trees (Riedmiller 1994).
Land clearing for agriculture can also cause loss of stability by causing change in the habitat. For example removal of woody vegetation in Australia, causing water levels to rise bringing salts closer to the surface of the soil reducing plant growth (Gordon et al. 2003). Intense weather, like drought, can also cause stability loss. Tilman and Haddi observed this in a fairly simple grassland experiment where different plots of land were kept and fenced of and only allowed water from precipitation and from the soil. The different amounts of precipitation per year were recorded. In years with drought, the land plots suffered species loss (D Tilman & Haddi 1992).
These different factors that lead to stability loss all seem to bring this about by causing the loss of species diversity. So the cause for ecosystem stability loss and loss of biodiversity seems to be almost inseparable.

Restoration of stability:

If loss of biodiversity is the most important aspect of reduced system stability, then stability might be repaired by the re-introduction of the species lost. Restoration is of course dependent on the ability of species to move, or be moved, to the depleted habitat and for the conditions to allow them to be able to compete within the new species distribution of the environment. Re-integration into a habitat can be accomplished in different ways.
If neighboring environments contain the same species that the reduced environment originally had, then the species from the neighboring environments might be able to migrate into the depleted system and thus accomplish re-integration of lost species. This has been shown to happen in Mongolia with former agriculture land. Abandoned cropland was being reclaimed by species of the surrounding grassland. Rodents cleared the area from dead plant material, creating open ground in which native grasses, coming in from the surrounding land, could grow(Yoshihara et al. 2009).
Re-introduction of species is dependent on how far a species can disperse itself. For redistribution over longer distances mobile link species are needed.
Mobile link species are species that link habitats through their mobility, connecting habitats farther away from each other. If link species, in their movements carry organisms they can constitute an important agent for a reintroduction of species that have been lost. Thus, they can play a significant role in the repair mechanism of system stability. A good example of this is in the case of the flying foxes that spread the seeds of certain liana plants. They do this by eating the fruits of the plant, but not digesting the seeds there in. The seeds are dispersed with the droppings of the bat (P. A. Cox et al.

1991; P. Cox & T Elmqvist 1992). In this way plants can be reintroduced in deplete environments that the bats visit. In these cases, the ability to re-stabilize a system is dependent on the biodiversity of outside habitats to which the ecosystem is linked.

A species can be helped back into the ecosystem by relieving pressure. This can best be done when its growth conditions are at its most favorable, for instance by making use of seasonal differences (Holmgren & Scheffer 2001). By relieving the pressure at its optimal conditions the species can gain in abundance rapidly. And it can do so with less chance that another species has a competitive advantage under the same conditions and thus push the target species away.

Can stability and resilience be improved?

Can enhancing species diversity strengthen the stability and resilience?
The stabilizing effect of biodiversity documented in experiments came from species native to the environment. I would assume that enhancing biodiversity with native species would be rather a form of ecosystem restoration, than stability strengthening. There are several ways in which diversity may affect system stability. It may do so by diversity of different species. It may also do so by diversity within one species.

Increasing diversity <u>within</u> species does seem to strengthen stability of that species. This is seen in fishery management programs to control Pacific salmon (*Oncorhynchus* spp.) for optimum production. It not only failed to prevent fish population decline. In fact it caused greater uncertainty for salmon, their ecosystems, and the people who depend upon them. These management programs - developed from agricultural models - devised methods to stabilize fish production at optimum levels. The programs were based on the assumption that salmon ecosystems are predictable, malleable, and infinitely resilient and, therefore, could be controlled for optimum fish production. The final effect was that the interventions, simplifying the complex structure of salmon populations and their habitats, eroded the resilience of salmon ecosystems (Bottom et al. 2009). An increase of genetic diversity within species, however, has shown to make the response variance of an ecosystem higher, giving it more stability(Healey 2009).

It has been argued that the introduction of new species can have negative influence on stability, because the introduction disturbs the – often very fine-tuned – structure of the food web(Goldschmidt et al. 1993). An additional species uses resources and that would mean fewer resources for native species (Huisman & Weissing 2000). However, fluctuations in population densities caused by competition over resources can allow for more species to coexist even with few resources. Generally, one would expect that - at equilibrium - the number of coexisting species could not exceed the number of limiting resources. Occasionally, however, a large number of species have been found to coexist on just a handful of resources. This is known as the plankton paradox and can be resolved by resource competition models, which generate oscillations and chaos when species compete for three or more resources (Huisman & Weissing 2000). Oscillations and chaotic fluctuations of each species give new species a chance to come in and coexist. As long as there is no competitive advantage of one species over the other for the limited resources, the new species should participate in the population oscillations that the rest of the competing species undergo.

Thus, to have a stable system, one sometimes needs *un*stable populations.

Resource competition may not be the only determining factor on if new species can coexist. Not just having a competitive edge in acquiring resources, but also other aspects like predator avoidance or the ability to cope with adverse weather conditions should affect stability.
The coexistence of a new species with native species in a new environment, will be determined by a number of factors. Factors with different weights. It is difficult to predict whether a new species can coexist. The web of interactions is complex and there are too many unpredictable variables. It is questionable whether it is even possible to know all necessary factors for the introduction of new species.

Conclusion

The evidence is in favor of biodiversity being responsible for ecosystem stability. A multitude of observations and experiments in various fields of study report a positive relation between diversity and stability. The changes in one environment can have profound effects on a completely different environment.
To truly be able to preserve and restore stability, understanding is needed of the causes of the stability loss. If the cause of loss of stability through loss of species is hunting or land clearing, it can be restored through re-immigration of the species from neighboring environments. But if the cause of loss is invasion of outside species or climate change, the chance that re-immigration will bring a lasting effect to the restoration of the environment is small. The cause of the species loss is still present. If this is the case, it is important that the resistance of the stability of neighboring environments is kept high, so that the causes of stability loss do not effect these environments.

Manipulating the conditions that invading species are exposed to, may help restoring system stability. Deliberately altering circumstances, for instance by increasing the interaction strength with predator species, may lessen the intruders' competitive advantage. This may lessen or possibly even nullify the destructive influence of the invasive species, eventually even allowing it to integrate in to the ecosystem.
Regardless of the specificity of the problem, actions taken will probably only come to fruition when full account is taken of dependency of species to each other.

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