

Freshwater ecosystems are particularly vulnerable to major changes in the structure of biological communities following small increases in stressors (tipping points).

Protecting against tipping points is a goal of environmental policy that seeks to limit environmental change to within acceptable bounds [1].

Identifying which particular characteristics of ecosystems underpin vulnerability will facilitate more directed management and better policy to protect against tipping points. We investigated [2] the attributes of freshwater ecosystems that increase their vulnerability to tipping points, especially situations where undesirable ecosystem changes become reinforced by feedbacks that make them particularly hard to reverse (known as hysteresis [3]).

What are tipping points?

Although it is tempting to see *any* rapid change in a freshwater ecosystem in response to increases in a stressor, such as nutrient concentrations, as a tipping point, it is particularly important to recognise the special characteristics of tipping points which make them particularly problematic. They are sudden thresholds associated with large non-linear changes in community structure and function following small increases in stressor values, and are underpinned by feedbacks [4].

The community structure and ecological feedbacks that characterise the degraded ecosystem state are different to those of the non-degraded ecosystem state. Thus restoration strategies that simply attempt to reduce the stressor to levels prior to the tipping point may fail because the structure and feedbacks of the degraded regime alter the system trajectory (i.e., producing hysteresis), necessitating stronger restoration measures.

A rapid change in an ecosystem over *time* may or may not be indicative of a tipping point; it primarily depends on the shape of the relationship between the stressor and the state of the ecosystem, and the presence of the feedbacks. The scientific literature abounds with discussion on this topic, but recent reviews clarify the terminology and encourage preventative actions [5, 6], and were the subject of a 2017 policy brief [7].

Habitat-forming organisms are the key

Our evaluation suggests that the potential for tipping-points in the responses of freshwater ecosystems to stressors is linked to the ability of habitat-forming organisms to modify habitats and thereby resist the effects of the stressor or other disturbances. Classic examples of tipping points include the sudden loss of water clarity and aquatic plants (also called 'macrophytes') following nutrient increases in shallow lakes [4, 8].

Here the macrophytes are the habitat-forming organisms. Clear water in shallow lakes can be maintained by feedbacks whereby the macrophytes stabilise sediments, compete with algae for nutrients and provide refuge for zooplankton against fish predation, thus contributing to low phytoplankton abundance and low water turbidity (Fig. 1). Alternatively, turbid-water states are maintained by high phytoplankton abundance which shades macrophytes leaving sediment unstable and prone to windinduced resuspension, and thus allows a larger pool of nutrients to be utilised by phytoplankton, exacerbating turbidity (Fig. 1).





Figure 1: Aquatic plants or 'macrophytes' (left), by binding sediment can reduce the availability of nutrients and water column turbidity caused by phytoplankton. The loss of such habitat-forming plants, as has occurred in Te Waihora – Lake Ellesmere (right), means wave action can easily suspend sediment and nutrients, leading to a turbid and algal-dominated lake.

The presence of these habitat-forming organisms, like the aquatic plants in lowland lakes, is a central feature that drives the feedbacks that lead to sudden changes in community structure and function that characterise aquatic tipping points.

The activities of these habitat-forming organisms, which modify physical conditions such as controlling the suspension on sediments in shallow lakes, can mitigate disturbances, especially those caused by changes in flow and wave action, and provide habitat for organisms such that the ecosystem has more resistance to a stressor until the tipping point is reached [9]. Although their role in shallow lakes is well understood, the influence of habitat-forming organisms in other freshwater ecosystems is less well known.

Nevertheless, extrapolation from case studies [10-12] suggests that where aquatic and riparian plants, or even algae,

substantially modify habitat conditions, tipping points could occur. In addition to macrophytes in lowland lakes, likely examples of these habitat-forming organisms in Aotearoa New Zealand include: non-native macrophytes which clog lowland agricultural waterways, aquatic plants and algae that provide habitat structure in alpine tarns, algal invaders like didymo (*Didymosphenia geminata*) that substantially modify river-bed habitats, moss and macrophytes which considerably enhance habitat heterogeneity in springs and other stable streams, and invasive riparian plants which, by altering river channel shapes, also potentially alter habitat conditions for aquatic organisms (Fig. 2).

The crucial impact of habitat-forming organisms on ecosystem resilience implies that close focus on those organisms will be particularly useful for anticipating tipping points in freshwater systems.



Figure 2: Possible habitat-forming freshwater taxa which likely underpin tipping points in New Zealand freshwater ecosystems include: non-native macrophytes (a), algae in tarns (b), didymo algae in rivers (c), aquatic plants in springs (d), and invasive riparian plants (e).

Predicting tipping point vulnerability

Our extrapolation from situations where tipping points have been confirmed, and from situations where habitat-altering organisms occur, suggests that physically benign freshwater habitats, especially spring-fed channels, lake outlets, shallow lakes, tarns, and dam tail waters, are likely to be most vulnerable to tipping points.

These ecosystems, because of their often stable flows, all provide conditions for habitat-forming organisms to dominate and thereby influence physical habitat conditions. In turn, stressors (or any influence) which affects the abundance of those habitat-forming organisms could lead to sudden changes in the structure and function of biological communities if a tipping point threshold is reached.

Research priorities

Defining where the thresholds in the abundance of the habitat-forming organisms which control tipping points occurs should be a key focus of research informing management of freshwater tipping points. Those thresholds are becoming better understood in lowland lakes, but in other habitats even the key stressors have not been defined.

Ecosystem tipping points are likely to be strongly linked to critical densities of those organisms [5, 13], so this is a key research gap needed to better understand and predict when tipping points will occur. Finally, further evaluating the range and distribution of habitat-forming organisms beyond the general list of habitats above will improve our ability to identify vulnerable freshwater ecosystems.

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