

Can algal uptake stop NO_3^- pollution?

ARISING FROM Cardinale, B. J. *Nature* **472**, 86–89 (2011)

The influence of biodiversity on ecosystem function has been of interest to community ecologists for decades. Recently, Cardinale¹ reported that biodiversity affects nitrate (NO_3^-) uptake in algal communities and that, as a result, biodiversity may help mitigate nutrient pollution. Although Cardinale's conclusions about niche partitioning are interesting (figure 2 in ref. 1), his extension of these findings to problems of nutrient pollution is premature. Algal uptake is only a short-term nitrogen sink; control of NO_3^- pollution requires long-term solutions.

Nitrate removal in streams typically occurs via two pathways. Denitrification is the microbial conversion of NO_3^- to N_2 gas (Fig. 1). This is the most important means of permanent NO_3^- removal from streams. However, it is not considered in Cardinale's study.

The second NO_3^- uptake pathway is assimilation by primary producers (in this case, algae). Algae acquire nutrients to fulfil physiological demands and support growth, but these same nutrients are later released after cell death or disruption (such as the brushing treatment applied to some flumes to create heterogeneity). Algal uptake leads to temporary storage of nitrogen in algal tissues (turn-over time ranges from ~ 17.5 –47 days^{2–4}), and can have significant short-term effects on nitrogen export to downstream ecosystems. But, because benthic algae do not accumulate over long (annual or inter-annual) periods, this uptake mechanism represents only a transient storage pool and thus has no enduring effect on downstream water quality (Fig. 1).

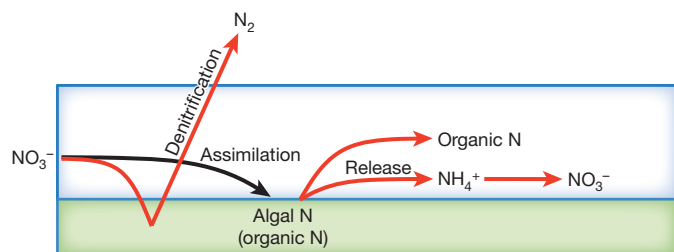


Figure 1 | Nitrogen cycling in streams. Red arrows indicate processes not measured by Cardinale¹. Storage in groundwater and sediments, N_2 fixation and fluxes to other ecosystems (for example, floodplains) may also occur.

Algae could potentially mediate permanent nitrogen removal in streams by facilitating increased rates of denitrification^{5,6}. Indeed, Cardinale's results raise the intriguing possibility that algal diversity could affect denitrification rates via changes in the availability of nitrogen, carbon or oxygen to denitrifiers. However, until this potential effect is demonstrated, conclusions about biodiversity effects on the control of aquatic nitrogen pollution are premature.

We agree with Cardinale that nitrogen enrichment threatens the integrity of aquatic ecosystems and that nitrogen removal is a critical ecosystem service provided by streams⁷. And, although Cardinale has elucidated a potential mechanism for biodiversity to influence stream nutrient cycling, for this work to be extended to pollution control in natural ecosystems it must be tested in environments incorporating critical biogeochemical pathways—namely, denitrification and nitrogen fixation—and it must consider long-term nitrogen dynamics.

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Cardinale reply

REPLYING TO H. M. Baulch, E. H. Stanley & E. S. Bernhardt *Nature* **477**, doi:10.1038/nature10418 (2011)

Over the last 20 years, 59 experiments have quantified how the richness of plants and algae influence concentrations of inorganic nitrogen in soil or water¹. Of these, 86% have shown that the concentration of nitrogen decreases as biodiversity increases—by an average of 48%. The primary contribution of my study² was to identify a biological mechanism that is likely to explain these biodiversity effects. Using stream mesocosms, I showed that the impacts of algal diversity on nitrogen dynamics are controlled by niche partitioning—a long presumed, but rarely demonstrated mechanism. Baulch, Stanley and

Bernhardt³ have questioned whether my findings have any implications for managing water quality in 'real' streams, as I suggested. They argue that nitrogen assimilation by algae cannot influence long-term nitrogen retention due to high turnover of algal biomass and rapid recycling of nitrogen, and they suggest that the only permanent loss of nitrogen from a stream is via denitrification.

Baulch, Stanley and Bernhardt³ are correct in saying that my study does not reveal the ultimate, long-term fate of nitrogen in streams. Although assimilation represents the critical first step in nitrogen

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removal from water, it must be followed by some other process that leads to long-term storage or permanent removal from a stream if there is to be any meaningful improvement in water quality. Increased rates of assimilation very likely increase the probability that other long-term mechanisms operate, but my study only explicitly linked diversity to assimilation. So I agree that researchers now need to take the next step and examine the impacts of biodiversity on additional pathways involved in the nitrogen cycle.

But as we take these next steps, I worry that Baulch, Stanley and Bernhardt³ have given an incomplete roadmap. From their comment, one might get the impression that everyone agrees on what processes control the fate of nitrogen in streams, and that denitrification is the sole process we need to focus on. I do not believe this to be the case.

Baulch, Stanley and Bernhardt³ present what I call the 'quasi-chemostat' model of a stream, which assumes that streams are in a steady state such that there is no net accrual of biomass, and no net storage of material. As nutrients flow into a stream, they are assimilated and remineralized at comparable rates by organisms with high turnover. The nutrients are not transformed in any way, such that nitrogen simply 'spirals' downstream in the same biologically active form. They argue³ that the one exception to these chemostat-like assumptions is that denitrification may transfer some nitrogen from the stream to air.

Many researchers, including myself, think that the quasi-chemostat model makes overly simplistic assumptions that are not supported by existing data. Dozens of ¹⁵N tracer studies have shown the following. First, assimilation accounts for an average of 84% of NO₃⁻ removal from stream water^{4,5}, whereas denitrification accounts for just 16%⁶. Second, up to 67% of assimilated nitrogen can go into primary consumers⁷ (a pathway that Baulch, Stanley and Bernhardt³ do not consider), much of which can be lost to terrestrial environments via emergence or consumption by terrestrial predators^{8,9}. Third, some studies indicate that 25% or more of imported nitrogen can end up in depositional habitats¹⁰ or hyporheic zones¹¹ where it has residence times on the scale of years^{12,13}. Last, several studies show that the vast majority of nitrogen that enters a stream reach is transformed and exported downstream in a particulate form that is less available for biological uptake^{7,12}.

These findings all violate the assumptions that Baulch, Stanley and Bernhardt³ have made about nitrogen cycling in streams. So although they make a useful point that we need to examine how biodiversity influences the suite of processes that influence the long-term fate of assimilated nitrogen, I believe that we would benefit from taking a broader view of the nitrogen cycle than depicted in figure 1 of Baulch, Stanley and Bernhardt³.

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