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Magnani *et al.* reply

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Nitrogen (N) deposition alters ecosystem function in several ways, with important effects on N leaching and water quality, as well as on interspecific competition and biodiversity. These changes have been attributed to ecosystem N saturation, defined as the alleviation of N limitations on rates of biological function¹. After an initial fertilization effect, N saturation has also been suggested to reduce plant function and growth², eventually leading to forest dieback. Although our observation of a substantial positive effect of N deposition on forest carbon (C) sequestration³ does not imply the absence of nitrate losses or other negative effects, as rightly stressed by De Schrijver *et al.*⁴, the sustained response observed demonstrates that the fear of a generalized forest decline in response to N fertilization could be overstated, at least within the rather broad N deposition range explored in our analysis. The nature of the observed response of forest C sequestration to N deposition, however, has been questioned outright by de Vries *et al.*⁵, who suggested that it could be an artefact resulting from the covariation between N deposition and other environmental variables. The arguments proposed against an overwhelming N effect, however, do not seem to stand up to close scrutiny.

We agree that ecosystem gross primary production (GPP) and plant growth are, to a large extent, controlled by local climate, drought and fertility (that is, N mineralization associated with soil organic matter decomposition), although fertility could be itself influenced by current and past N deposition⁶. However, the same environmental factors would modulate in parallel ecosystem respiration, and as a result do not seem to affect net ecosystem production (NEP), which is the difference between GPP and ecosystem respiration and is the subject of our analysis³. Both components of NEP seem to be also affected by N deposition, but in opposite directions: apart from the positive effects on plant growth considered by de Vries *et al.*⁵, respiration is known to be significantly reduced by N fertilization, as demonstrated by manipulation experiments^{7,8} as well as regional transect studies⁹. The combined effect at the ecosystem level is largely missed when focusing on tree growth alone.

The question remains of the magnitude of the observed response to N deposition. Assuming a linear relationship between NEP and N

deposition, a slope of 445 ± 38 kg C per kg N of wet N deposition can be inferred from our entire data set ($n = 20$, rather than the subsample of 8 data points in the analysis by de Vries *et al.*⁵). If we assume, rather conservatively, that wet deposition constitutes 40–50% of total N deposition¹⁰, this would imply a NEP sensitivity to total N deposition of approximately 175–225 kg C per kg N, which is consistent with the stoichiometry of plant tissues and soil organic matter. Although it is true that fine roots account for a significant fraction of forest growth, it should be noted that one of the main effects of increased N availability is an increased allocation to woody tissues (with a high C:N ratio of up to 500:1) away from fine roots¹¹. This mechanism could indeed represent an important component of the observed response to N deposition.

Far from implausible, a 200:1 sensitivity is nevertheless higher than suggested by long-term forest fertilization experiments¹². Potential problems with N manipulation studies have already been discussed¹³. In particular, they overlook the role of canopy N uptake, which enables plants to absorb a relevant fraction of incoming N without any competition from soil microbes. Canopy N uptake amounts to up to 70% of N deposition, providing as much as one-third of tree N requirements^{9,14,15}. The critical comparison of results from ecosystem manipulation and observational studies could be providing a rare, unforeseen insight into the key factors controlling C–N relations in forest ecosystems.

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