

flow regime ($Q = 178 \text{ m}^3 \text{ s}^{-1}$) with the river flow velocity (u) of 0.49 m s^{-1} . The overall attenuation times (t_{overall} , days) from the combined effect of volatilization and degradation (Figure 1a), as well as the ratio between the attenuation times from volatilization (t_{vol}) over the attenuation times from degradation (t_{deg}) (Figure 1b), are shown. Attenuation times by volatilization are longer (degradation will be the faster removal mechanism) for chemicals with low to medium volatility (the air–water [a_w] partition coefficient $-4 < \log K_{a_w} < -2$) and with low hydrophobicity (the octanol–water [ow] partition coefficient $0 < \log K_{ow} < 4.5$). Conversely, attenuation times from volatilization are shorter (the compound remains for less time in water) for compounds with $0.5 < \log K_{a_w} < 2$ and $0 < \log K_{ow} < 8$. However, channelization, tile drains, or flooding will increase stream flow, thereby decreasing the retention time and potential to attenuate pollutants through biodegradation.

Natural attenuation processes like volatilization and degradation can decrease the concentration of pollutants considerably (tens of kilometers away from their source of input) and serve to moderate organic pollutant outputs to seas and oceans, according to RIOPOP. For example, dissolved polychlorinated biphenyl concentrations decreased from upstream to downstream in the Delaware River from 1200 to 420 picograms per liter (Rowe *et al.* 2007) and in the Ebro River from 43–108 nanograms per liter (ng L^{-1} ; Fernández *et al.* 1999) to 8.9 ng L^{-1} (Gómez-Gutiérrez *et al.* 2006), which is consistent with volatilization losses. Alkylphenol concentrations in the Hudson River also decreased from upstream to downstream by well-documented degradation processes (Van Ry *et al.* 2000). On the other hand, volatilized chemicals can be deposited to nearby or remote watersheds (Berglund 2003), thus limiting the effectiveness of management strategies at the watershed level and pointing to one “global watershed” for semi-volatile organic pollutants.

The ubiquitous and complex nature of these attenuation processes has made it difficult to estimate the potential of natural attenuation in mitigating organic chemical contamination close to and downstream from pollution sources. The characterization of riverine attenuation processes such as biodegradation and biotransformation can provide insights for possible bioremediation strategies. Through mutating or acquiring degradative genes, these bacteria can adapt and proliferate in the environment as a result of the selection pressures created by the pollutants (Van der Meer 2006). The study of pollutant cycling and bacterial response to organic pollutants will improve current riverine pollution remediation strategies and management tools.

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doi:10.1890/12.WB.017



Non-native species promote trophic dispersion of food webs

Peer-reviewed letter

Estes *et al.* (2011) reported that the loss of large apex consumers has drastically altered ecosystem functioning worldwide, through the mechanism of “trophic downgrading”, and urgently appealed for interdisciplinary research to forecast the effects of this phenomenon on ecosystem process, function, and resilience. Although we agree with the authors’ premise that the “loss of apex consumers is arguably humankind’s most pervasive influence on the natural world”, this study and others continue to account for only one side of the biodiversity ledger – by failing to recognize that humans often select for and introduce large-bodied non-native species, which frequently replace lost native predators (Eby *et al.* 2006; Byrnes *et al.* 2007; Blanchet *et al.* 2010). For instance, the worldwide introductions of predatory mammals on islands represent new upper-trophic-level species. The reality is that non-native species now represent a substantial fraction of local and regional diversity (Sax *et al.* 2002; Leprieur *et al.* 2008) and have led to both the extirpation of native species (Clavero and García-Berthou 2005) and the replacement or addition of new apex consumers (Griffiths *et al.* 2010; Schlaepfer *et al.* 2011). Although trophic downgrading of native communities has undoubtedly occurred, the potential functional compensation repre-

sented by the introduction of non-native species has yet to be fully appreciated (Wardle *et al.* 2011).

Here, we tested whether the addition of non-native species can compensate for native species loss and resultant trophic downgrading of food webs. We used freshwater fishes as a model system because non-native introductions of such organisms are widespread, yet variable, and have modified the trophic structure of countless ecosystems worldwide (Leprieur *et al.* 2008; Cucherousset and Olden 2011). To do so, we collected information on the presence of native and non-native fish species from 13 watersheds. Watersheds were selected to be widely distributed across the globe and have comprehensive fish species' lists (additional information available in WebTable 1). For each species, we recorded its trophic position based principally on diet studies (www.fishbase.org). Although we acknowledge that local environmental conditions and time since introduction could affect these estimated trophic positions, the selected variables provide an opportunity to perform large-scale comparisons of trophic structure. We then characterized the trophic structure in the historical period before species introductions (ie current native species only, assuming no extinction within the watershed) and in the contemporary period after species introductions (ie current native and non-native species) using an equal weighting of the trophic position for each species in each watershed.

Nine out of 13 watersheds showed evidence of a slight increase in mean trophic position in response to non-native species introductions, although overall the change in the contemporary time period was modest and not statistically significant (paired *t* test, $t_{12} = 1.38$, $P = 0.19$; Figure 1a). This reflects the fact that the mean trophic position of native versus non-native species did not differ significantly (paired *t* test, $t_{12} = 0.34$, $P = 0.74$). An interesting, but somewhat unexpected, finding was that

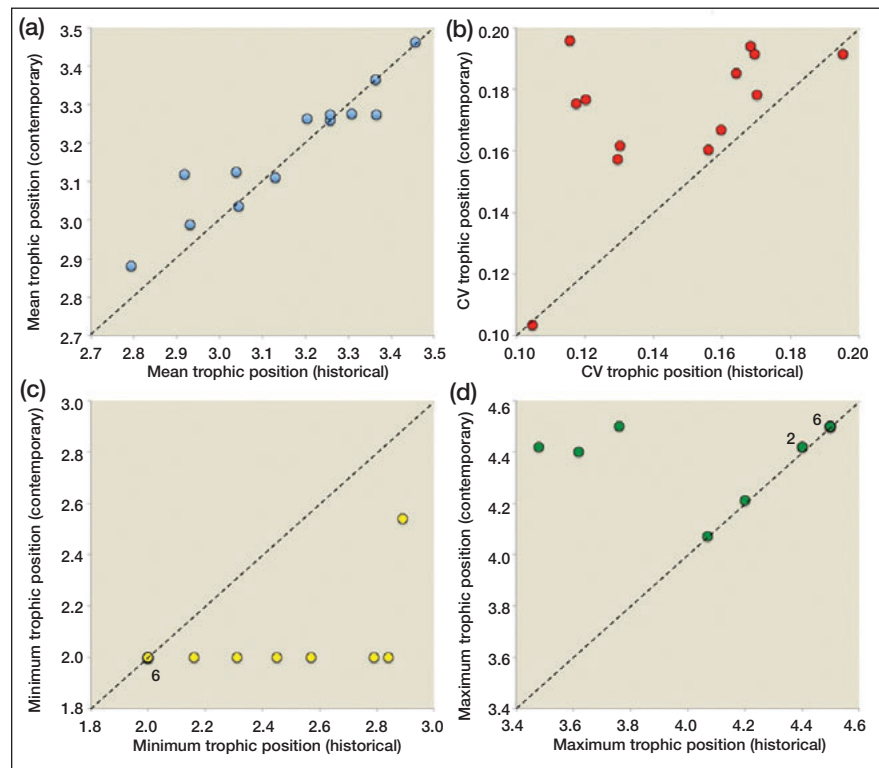


Figure 1. (a) Mean, (b) coefficient of variation (CV), (c) minimum, and (d) maximum trophic position of freshwater fish in the historical period before species introductions (ie current native species only, x-axis) and in the contemporary period after species introductions (ie current native and non-native species, y-axis) in the 13 studied watersheds. When displayed, the values in the panels indicate the number of overlapping points.

the introduction of non-native species significantly increased the variability of the trophic position (ie “trophic dispersion”): a consistent and significant pattern across all watersheds (paired *t* test, $t_{12} = 3.68$, $P < 0.01$; Figure 1b). This pattern is driven by the fact that non-native fish species in both upper and lower trophic positions have been introduced to freshwater ecosystems (Eby *et al.* 2006; Gido and Franssen 2007; Cucherousset and Olden 2011), with all food webs decreasing (or showing no change) in their minimum trophic position (Figure 1c) and increasing (or showing no change) in their maximum trophic position (Figure 1d).

Our investigation of freshwater fishes across the world suggests that the introduction of non-native species might, as predicted, increase the length of food chains through the introduction of top predators and, unexpectedly, modify the basal struc-

ture of food webs through the introduction of herbivorous fish species. Blanchet *et al.* (2010) found that introduced fish species had significantly larger body size than native species as a consequence of human selection for aquaculture and angling (Eby *et al.* 2006; Gozlan 2008). Apparently this subset is composed of both large-bodied predators (high trophic position, eg salmonids, centrarchids) and large-bodied herbivorous species (low trophic position, eg cyprinids, cichlids), leading to the observed trophic dispersion of food webs. A similar pattern occurs for terrestrial mammals on islands with the introduction of large predatory and herbivorous species worldwide (eg Courchamp *et al.* 2003; Maron *et al.* 2006). Biological invasions interact synergistically, antagonistically, and/or additively with multiple human-induced impacts on ecosystems (Strayer 2010), and their effects on food-web structure could be idiosyncratic. How-

ever non-native species, through the simultaneous addition of species in high and low trophic positions into recipient ecosystems, may be promoting greater trophic variability and mitigating trophic downgrading caused by native species loss. Therefore, the process of trophic downgrading highlighted by Estes *et al.* (2011) may not be a general rule but is likely the exception in a world increasingly being threatened by non-native species.

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The research leading to these results has received funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant agreement number PERG08-GA-2010-276969.

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doi:10.1890/12.WB.018



Reply to Cucherousset *et al.*

We agree that non-native predators have strongly influenced the structure and function of nature in many places. We are skeptical, however, of the authors' implication that these non-native predators are functional equivalents of those that have been lost. The fundamental problem is that mean trophic level and food chain length do not reflect the complex ways in which the influences of predators spread through food webs, nutrient cycles, and other ecosystem processes.

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doi:10.1890/12.WB.019

Erratum

In Greaver *et al.* (2012; 10[7]: 365–72), panel headings and selected y-axis labels in Figure 2 on page 367 were incorrectly matched with their respective panels. A corrected version of the figure appears below.

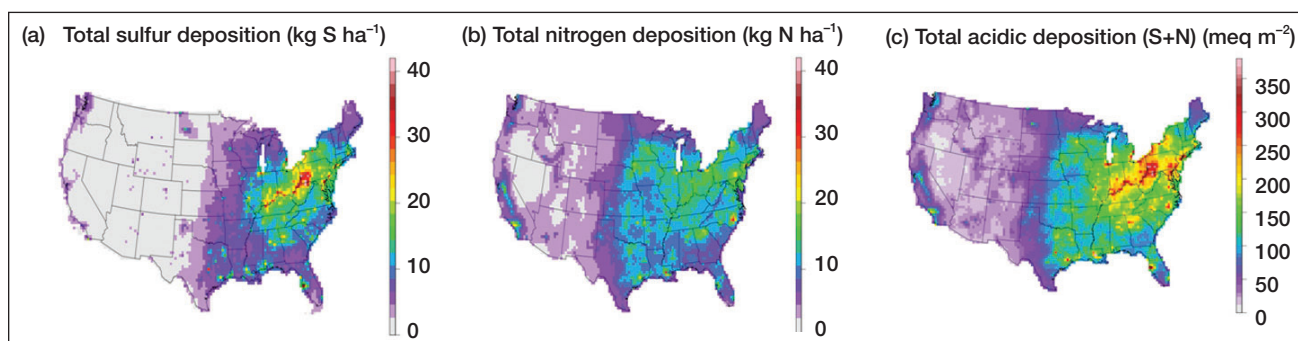


Figure 2. Maps of CMAQv4.7.1 estimates of annual (a) sulfur, (b) inorganic nitrogen, and (c) acidic deposition for 2002 for a 12-km grid over the continental US, where wet deposition is adjusted by the ratio of observed to modeled precipitation and then regionally corrected for wet deposition bias, and where observed precipitation is from the Parameter-elevations Regressions on Independent Slopes Model.