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Taxonomic resolution and treatment effects – alone and combined – can mask significant biodiversity reductions

Claudio Bozzuto [1,2] & Wolf U. Blanckenhorn [1*]

[1] Institute of Evolutionary Biology and Environmental Studies, Winterthurerstrasse 190, 8057 Zurich, Switzerland.

[2] Current address:

Wildlife Analysis GmbH, Oetlisbergstrasse 38, 8053 Zurich, Switzerland.

Supplementary material:

Additional methods and results: inclusion of competition (with Figures A1- A3).
Figures A1 – A3, S1 – S2.
Tables S1 & S2.

Additional methods and results: inclusion of competition.

As introduced in the main text, in the following paragraphs we explore how under simplified assumptions the inclusion of interspecific competition, in conjunction with treatment effects and taxonomic resolution, affects biodiversity indices. We analyse situations where only species within a genus compete for the same resources because they are ecologically similar, and that both species are equal competitors. Throughout this study, we treat only this (restrictive) case of within genus competition, for simplicity referred to as competition, well aware that competition often also takes place among distantly related species (Marquet 1990), with different competitive abilities involved that may additionally vary over time (Connell 1983).

Methods

To study the effect of competition, we apply the concept of press perturbation (Bender 1984). For the simple situation here of one genus with two competing species, this implies that when one species is reduced in abundance due to treatment, the other species shifts to a higher equilibrium value.

We apply a simple Lotka-Volterra competition model to calculate the modified equilibrium densities. The scaled system without treatment for two equally good competitor species is given by eq. 11:

$$\begin{aligned}\frac{dX}{dt} &= 1-(X+\gamma Y)\\ \frac{dY}{dt} &= 1-(Y+\gamma X)\end{aligned} \tag{11}$$

Without treatment both species would attain the same equilibrium value $E = 1/(\gamma + 1)$. However, in case one competing species is affected by treatment, its abundance is kept at $E_t = \alpha E$, whereas the congeneric species will reach the new equilibrium value $E' = 1 - \alpha\gamma/(\gamma + 1)$. For such a competitive system to have a stable non-trivial equilibrium point, all interaction strength parameters must be smaller than 1. Nonetheless, to simplify the following equations, we chose parameter values of 1. In dynamical terms this turns the equilibrium point into a half-stable one, in this case $E_t = \alpha/2$ and $E' = 1 - \alpha/2$. By choosing a carrying capacity of $K = 2n$, and noting that E_t and E' represent proportions, the equilibrium abundances are given by $n_t = \alpha n$, and $n' = n(2 - \alpha)$.

Next, we derive the diversity index when all species are determined at species level. Three cases have to be considered: a) no species in a genus is affected by treatment, b) both species are affected by treatment, and c) only one of the species is affected by treatment. For case c), both equilibria n_t and n' are relevant, for case a) none of them is relevant, and for case b) the same equilibrium n_t is relevant for both species. The total number of individuals is $\bar{N} = \big(S(1-\delta) - S\delta(1-\psi)\big)n + Sn\alpha\delta\psi + Sn\alpha\delta(1-\psi) + Sn(2-\alpha)\delta(1-\psi)$, which can be simplified to $\bar{N} = N\big(1 + \delta\psi(\alpha - 1)\big)$. For the latter case we write $\bar{N} = Nh$, also used for eq. 16. Thus, the equation for the Simpson-index with competition includes on the right side, from left to right (eq. 12): (i) unaffected species (without competition), (ii) affected species (without competition), (iii) affected species (with competition), and (iv) unaffected species (with competition).

$$
{}_{t+c}^{0L}\lambda = \left(S(1-\delta) - S\delta(1-\psi)\right)\left(\frac{n}{\bar{N}}\right)^2 + S\delta\psi\left(\frac{\alpha n}{\bar{N}}\right)^2 + S\delta(1-\psi)\left(\frac{\alpha n}{\bar{N}}\right)^2 + S\delta(1-\psi)\left(\frac{(2-\alpha)n}{\bar{N}}\right)^2 \quad (12)
$$

Rearranging and simplifying eq. 12 leads to eq. 13:

$$
{}_{t+c}^{0L}\lambda = \lambda_0\left(\frac{1+\delta(\alpha^2-1)}{h^2} + \frac{\delta(1-\psi)((2-\alpha)^2-1)}{h^2}\right) \quad (13)
$$

If $\psi = 1$, then ${}_{t+c}^{0L}\lambda$ reduces to ${}_{t}^{0L}\lambda$. If $\psi = 0$, eq. 13 reduces to:

$$
{}_{t+c}^{0L}\lambda_{\psi=0} = \lambda_0(1 + 2\delta(\alpha-1)^2) \quad (14)
$$

The last case we discuss includes competition *and* taxonomic resolution. Here again we make the assumption of a strong phylogenetic signal (see explanation for eq. 9 above), but only in part. Obviously, competition effects are only expressed if only one (of two) species is affected by treatment, so the strong assumption does not make sense at this level. However, for the binning process the reduced abundance of an affected species plus the increased abundance of its competitive congener result in the same total abundance at genus level as for two unaffected species taken together, namely $2n$. The above-mentioned partial assumption of a strong phylogenetic signal thus means that for all genera whose species are *not* competitors we make the strong assumption: both species are or are not affected by treatment.

The equation for the Simpson-index including competition and taxonomic resolution includes on the right side, from left to right (eq. 15), with $\bar{N}$ as defined for eq. 12: (i) unaffected species at species level, (ii) unaffected species at the higher level, (iii) affected species (without competition) at species level, (iv) affected species (without competition) at a higher level, (v) unaffected species (with competition) at species level, (vi) affected species (with competition) at species level, and (vii) mixed affected/unaffected species (with competition) at a higher level.

$$
\begin{aligned}
&{}^{1L}_{t+c}\lambda \\
&= (S(1-\delta) - S\delta(1-\psi) - b2^u)\left(\frac{n}{\bar{N}}\right)^2 + b\left(\frac{2^u n}{\bar{N}}\right)^2 + (S\delta\psi - b_\delta 2^u)\left(\frac{\alpha n}{\bar{N}}\right)^2 \\
&+ b_\delta\left(\frac{2^u \alpha n}{\bar{N}}\right)^2 + \left(S\delta(1-\psi) - b_\psi 2^{u-1}\right)\left(\frac{\alpha n}{\bar{N}}\right)^2 \\
&+ \left(S\delta(1-\psi) - b_\psi 2^{u-1}\right)\left(\frac{(2-\alpha)n}{\bar{N}}\right)^2 + b_\psi\left(\frac{2^u n}{\bar{N}}\right)^2
\end{aligned} \tag{15}
$$

Rearranging and simplifying eq. 15 leads to eq. 16:

$$
\begin{aligned}
&{}^{1L}_{t+c}\lambda \\
&= \lambda_0\left(\frac{1+\delta(\alpha^2-1)}{h^2} + \frac{\delta(1-\psi)((2-\alpha)^2-1)}{h^2} + \frac{(b+\alpha^2 b_\delta)2^{u-d}(2^u-1)}{h^2}\right. \\
&\left. + \frac{b_\psi 2^{u-d}(2^u - 2(\alpha-1) - \alpha^2)}{h^2}\right)
\end{aligned} \tag{16}
$$

If $\psi = 0$, and hence $b_\delta = 0$, meaning that all affected species have a congener that is not affected, eq. 16 reduces to:

$$ {}^{1L}_{t+c}\lambda_{\psi=0} $$

$$ = \lambda_0\left(1 + 2\delta(\alpha-1)^2 + 2^{u-d}(2^u-1)\left(b + \frac{b_\psi(2^u - 2(\alpha-1) - \alpha^2)}{(2^u-1)}\right)\right) \tag{17} $$

Results

All Specimens Determined to Species Level

Fig. A1a shows the effect of treatment alone (same as Fig. 3a) and Fig. A1b the effect of treatment in combination with competition, i.e. ${}^{0L}_{t+c}\lambda^{-1} - {\lambda_0}^{-1}$ (eqs. 13 & 4), both as contour plots with species mortality (δ) and individual survival (α) as axes. δ in Fig. A1b stops at 0.5 because we chose $\psi = 0$, i.e. every genus contained one affected species and one unaffected congener. For all combinations of δ and α the inclusion of competition (Fig. A1b) always leads to a greater reduction in biodiversity, except for all α with $\delta = 0$ and for all δ with $\alpha = 0$.

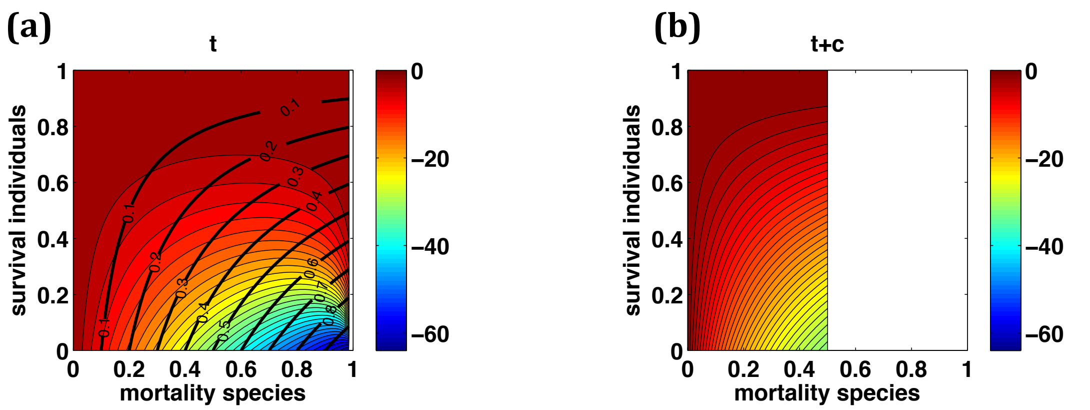

Fig. A1. (a) Contour plots of the reduction in diversity as a function of treatment (t) when all specimens are determined to species level, and **(b)** for the combined effect of t[reatment] *and* c[ompetition within genus] (t+c). In (a) an additional contour plot is overlaid showing the proportional reduction in total number of individuals. Species mortality (δ) is on the x-axis and individual survival α on the y-axis.

Taxonomic Resolution

Fig. A2 shows the reduction in diversity when (i) including treatment (left column contour-plots a - c), and (ii) for the combined effects of treatment and competition (right column contour-plots d - f); left column panels are the same as in Fig. 5 (left column). The corresponding eqs. 10 and 13 allow including taxa at *one* higher taxonomic level that (i) contain unaffected species (parameter b), (ii) contain affected species (b_δ), or (iii) contain species with competition (b_ψ), alone or in combination. Fig. A3 shows the same constellation, but with all higher taxa at family level. To permit direct comparison between taxonomic levels, in Fig. A3 we always used half of the values used at genus level (Fig. A2), as in our symmetrical tree (Fig. 1b) two genera bin into one family. For illustrative purposes we chose the particular combinations leading to the three contour-plots in each column of Figs. A2 & A3. If b_δ and b_ψ are greater than 0, then the proportion of species affected $\delta > 0$ is a function of these taxa and their taxonomic level (Table 1). Therefore the plotted values in Fig. A2b,c,e,f and A3b,c,e,f start at $\delta > 0$ (x-axis).

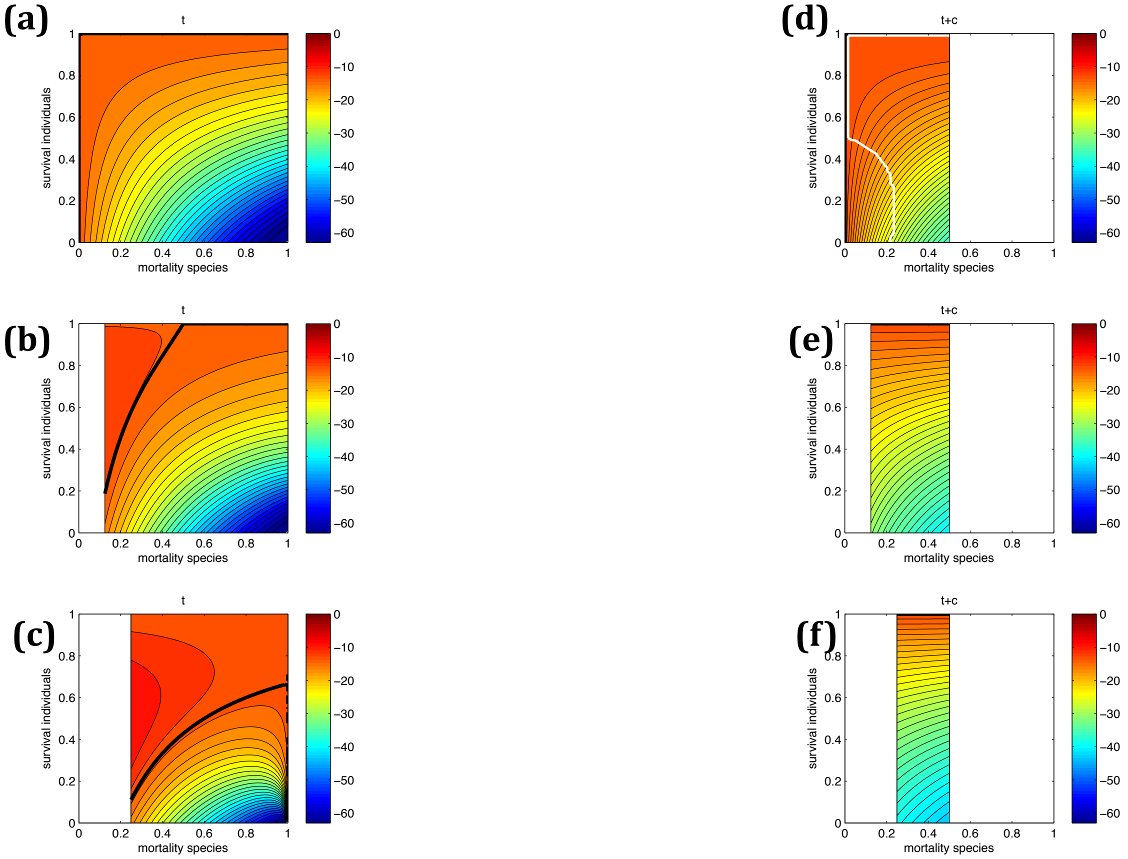

Fig. A2. Contour plots of the reduction in diversity as a function of taxonomic resolution and treatment (left column), and for the combined effects of treatment (t), taxonomic resolution, and within genus competition (right column: t+c), with all higher taxa (here 8) at genus level. Species mortality (δ) is on the x-axis and individual survival (α) on the y-axis. Parameter combinations: **(a,d)** all higher taxa unaffected: b = 8, $b_\delta = b_\psi$ = 0; **(b,e)** four taxa affected ($b = 4$) and four unaffected ($b_\delta = b_\psi = 4$); **(c,f)** all taxa affected: b = 0, $b_\delta = b_\psi$ = 8. Solid black lines: contour levels when only considering taxonomic resolution effects. Solid white lines: reduction when treatment (in the left column, same row) equals that with treatment and competition (in the right column). If b_δ and b_ψ are greater than 0, then the proportion of species affected $\delta > 0$ is a function of these taxa and their taxonomic level (Table 1); therefore the plotted values in Figure A3b,c,e,f start at $\delta > 0$ (x-axis).

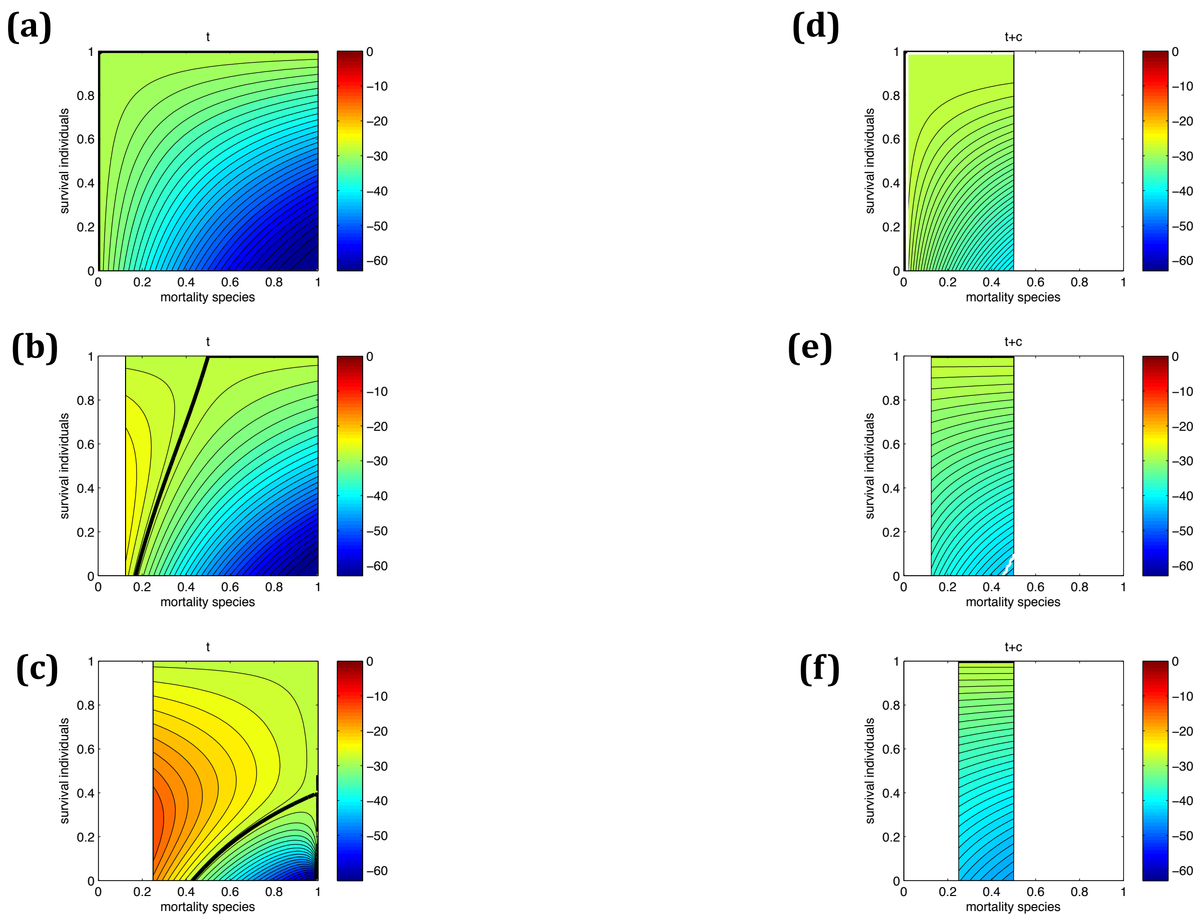

Fig. A3. Contour plots of the reduction in diversity as a function of taxonomic resolution and treatment (left column), and for the combined effects of treatment (t), taxonomic resolution, and within genus competition (right column: t+c), with all higher taxa (here 4) at genus level. Species mortality (δ) is on the x-axis and individual survival (α) on the y-axis. Parameter combinations: **(a,d)** all higher taxa unaffected: $b = 4$, $b_\delta = b_\psi = 0$; **(b,e)** two taxa affected ($b = 2$) and two unaffected ($b_\delta = b_\psi = 2$); **(c,f)** all taxa affected: $b = 0$, $b_\delta = b_\psi = 4$. Solid black lines: contour levels when only considering taxonomic resolution effects. Solid white lines: reduction when treatment (in the left column, same row) equals that with treatment and competition (in the right column). If b_δ and b_ψ are greater than 0, then the proportion of species affected $\delta > 0$ is a function of these taxa and their taxonomic level (Table 1); therefore the plotted values in Figure A3b,c,e,f start at $\delta > 0$ (x-axis).

Figures A2 & A3 show three main responses of our biodiversity measure resulting from including competition. (1) For most treatment combinations the additional inclusion of competition leads to a more pronounced decrease in diversity, except when higher taxa contain only unaffected species (top row in Figs. A2 & A3). In this case either all combinations including competition show less reduction in biodiversity (Fig. A3d, family level), or all combinations in the area right of the white line show less reduction (Fig. A2d, genus level). The second exception is the small fraction of combinations in Fig. A3e delimited by the white line (bottom-right corner). (2) The thick black contour lines in Figs. A2 & A3 delineate the sole effect of taxonomic resolution with 8 (4) taxa at the genus (family) level. From top to bottom in Figs. A2a-c, a decrease in unaffected (b) and corresponding increase in affected taxa (b_δ) at the higher taxonomic level leads to less reduction in biodiversity for an increasing set of combinations of α and δ (towards the upper left in Figs. A2a-c). This effect is even more pronounced at the family level compared to the genus level (cf. Fig. A2a-c & A3a-c), and does not show in Figs. A2d-f and Figs. A3d-f when competition is additionally included (b_ψ). (3) When augmenting the number of taxa at the higher taxonomic level that include either affected species or species suffering from competition (i.e. from top to bottom), the results in the left and right columns of Figs. A2 & A3 increasingly diverge. In the left column (without competition) the aforementioned introduces strong nonlinearities, and overall diminishes the reduction in diversity (compare contour plot colour bars with the same scale). This effect is absent in the right column when competition is additionally included.

Discussion

When not considering taxonomic resolution, adding competition led to additional reductions in diversity beyond those exerted by treatment (Fig. A1). This results because competition, as defined in this study, introduces within-genus variation, and consequently overall unevenness. Although in our analytical approach competition can be varied by changing the parameter ψ, we only showed results for $\psi = 0$, the situation when every genus contains one unaffected and one affected species. This implies that, as every affected species is reduced in abundance by the treatment, the corresponding competing species rises in abundance in a compensatory way due to competitive release, thus resulting in a less even community abundance distribution with a lower diversity index compared to the equivalent situation without competition ($\psi = 1$).

When treatment and taxonomic resolution effects are further combined with competition, the overall picture gets more varied and rather difficult to explain without resorting to the analysis of the underlying equations (avoided here). First, when all higher taxa comprise only unaffected species, the addition of competition attenuates the diversity reduction for some (genus-level: Fig. A2a vs. d) or all parameter combinations (family-level: Fig. A3a vs. d). However, when the number of unaffected taxa at the higher level decreases by including more affected taxa (Figs. A2b,c,e,f & A3b,c,e,f), competition almost always further reduces biodiversity (exception depicted in Fig. S3e). Second, compared to the situation with ideal taxonomic resolution (solid black contour lines in Figs. A2 & A3), adding competition prevents the above-mentioned smaller diversity reduction due to treatment (compare red shadings above the black line in Fig. A2b,c to Fig. A2e,f, where the black line is situated at the top of the graph at 100% individual survival). Third, no strong nonlinearities appear when introducting competition (in fact, they disappear: compare right and left columns in Figs. A2 & A3). This occurs because the combined abundances of two congeners experiencing competition, with only one being affected by treatment, result in the same total abundance as two unaffected congeners. Thus, augmenting the number of taxa at the higher level including competition has qualitatively similar effects as when substituting higher unaffected taxa with affected ones (Figs. A2 & A3, top to bottom). Hence, a negative effect of a treatment on one species will remain undetected in practice if species are binned because of compensatory competitive replacement by the closely related unaffected species. Nevertheless, addition of within-genus competition as treated in this study in general attenuates possible effects of treatment mortality on diversity, potentially also disabling strong nonlinearities.

Additional references

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Connell, J. H. 1983. On the Prevalence and Relative Importance of Interspecific Competition: Evidence from Field Experiments. The American Naturalist, 122:661-696.

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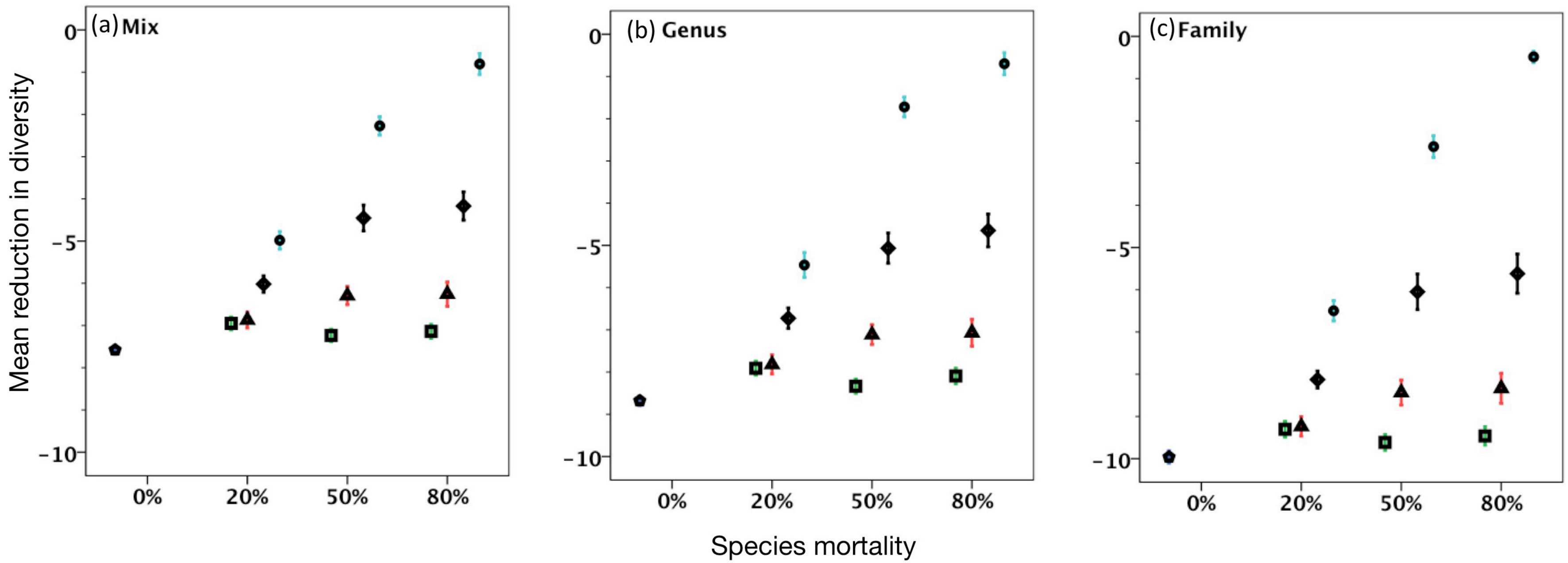
Table S1: Analysis of variance table testing for the combined effects of species mortality (3 levels), individual mortality (4 levels) and (a) 4 raw taxonomic levels (repeated measure: baseline species, genus, family, and mixed; corresponding to Fig. 2) on the simulated diversity index ${}^2D$, and (b) of 3 taxonomic levels (mixed, genus, family) on the *reduction* in the simulated diversity index ${}^2D$ relative to the baseline species level (corresponding to Fig. 3).

	(a)				**(b)**			
Source	***df***	***MS***	***F***	***P***	***df***	***MS***	***F***	***P***
Taxon level	3	2283.86	4563.23	<0.001	2	175.44	1361.22	<0.001
Taxon level * species mortality	6	22.52	44.99	<0.001	4	2.66	20.66	<0.001
Taxon level * individual mortality	9	76.26	152.36	<0.001	6	8.12	63.01	<0.001
Taxon level * species * individual mortality	18	6.85	13.69	<0.001	12	0.88	6.83	<0.001
Error (Taxon level)	807	0.50			538	0.129		
Species mortality	2	370.54	47.22	<0.001	2	248.90	50.03	<0.001
Individual mortality	3	825.84	105.24	<0.001	3	850.12	170.88	<0.001
Species * individual mortality	6	123.4	15.73	<0.001	6	75.21	15.11	<0.001
Error overall	269	7.85			269	4.96		

Table S2: Analysis of variance table testing for the combined effects of species mortality (3 levels), individual mortality (4 levels) and (a) 4 raw taxonomic levels (repeated measure: baseline species, genus, family, and mixed; corresponding to Fig. 2) on the simulated diversity index ^{1}D, and (b) of 3 taxonomic levels (mixed, genus, family) on the *reduction* in the simulated diversity index ^{1}D relative to the baseline species level (corresponding to Fig. 3).

	(a)				**(b)**			
Source	***df***	***MS***	***F***	***P***	***df***	***MS***	***F***	***P***
Taxon level	3	4329.56	13308.44	<0.001	2	2119.2	11951.25	<0.001
Taxon level * species mortality	6	25.96	79.78	<0.001	4	12.22	68.93	<0.001
Taxon level * individual mortality	9	102.05	313.69	<0.001	6	44.75	252.35	<0.001
Taxon level * species * individual mortality	18	9.43	28.99	<0.001	12	4.05	22.82	<0.001
Error (Taxon level)	879	0.33			586	0.177		
Species mortality	2	829.40	120.53	<0.001	2	213.69	85.98	<0.001
Individual mortality	3	2253.45	327.46	<0.001	3	866.63	348.70	<0.001
Species * individual mortality	6	292.61	42.52	<0.001	6	80.81	32.52	<0.001
Error overall	293	6.88			293	2.49		



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232 **Figure S1.** Mean (± SE) effect of species mortality level (x-axis) and individual mortality level within species (from left to right: 25% (squares),
233 50% (triangles), 75% (diamonds), 100%(circles)) on the *reduction* in simulated biodiversity index ${}^{2}D$ relative to the baseline, full-knowledge
234 species level situation per treatment combination (i.e. deducting the values given in Figure 2a in all cases) for the (a) mixed (left), (b) genus level
235 (center), and (c) family level (right) analyses. The pentagon to the left defines the baseline diversity without any mortality.

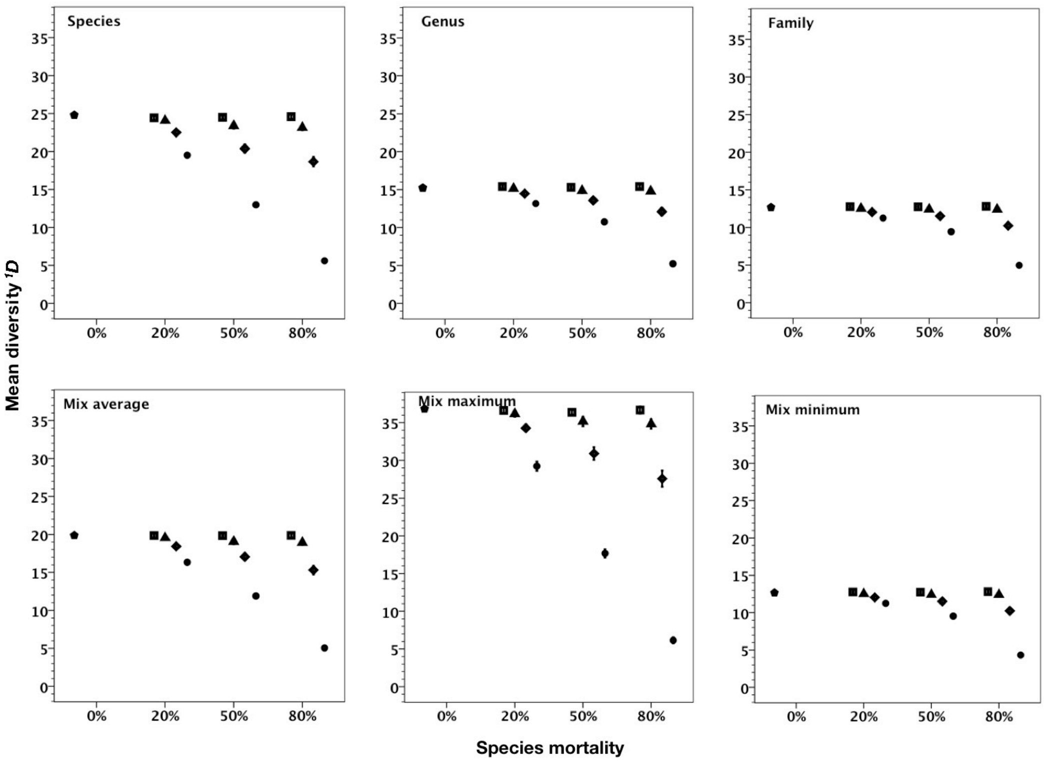

Figure S2. Mean (± SE) effect of species mortality level (x-axis) and individual mortality level within species (from left to right: 25% (squares), 50% (triangles), 75% (diamonds), 100%(circles)) on the simulated diversity index ${}^{1}D$ for the (a) baseline, full-knowledge species level, (b) genus level, and (c) family level, as well as for the (d) average, (e) maximal, and (f) minimal taxonomic mixes when considering all possible combinations of taxonomic resolution and treatment. The pentagon to the left defines the baseline diversity without any mortality.