

The importance of ecological networks in multiple-stressor research and management

Andreas Bruder^{1, 2}, André Frainer^{3, 4*}, Thibault Rota⁵, Raul Primicerio³

¹University of Applied Sciences and Arts of Italian Switzerland, Switzerland, ²University of Applied Sciences and Arts of Italian Switzerland, Switzerland, ³UiT The Arctic University of Norway, Norway, ⁴Norwegian Institute for Nature Research (NINA), Norway, ⁵Université Toulouse III Paul Sabatier, France

Submitted to Journal:
Frontiers in Environmental Science

Specialty Section:
Environmental Toxicology

ISSN:
2296-665X

Article type:
Perspective Article

Received on:
04 Jan 2019

Accepted on:
17 Apr 2019

Provisional PDF published on:
17 Apr 2019

Frontiers website link:
www.frontiersin.org

Citation:
Bruder A, Frainer A, Rota T and Primicerio R(2019) The importance of ecological networks in multiple-stressor research and management. *Front. Environ. Sci.* 7:59. doi:10.3389/fenvs.2019.00059

Copyright statement:
© 2019 Bruder, Frainer, Rota and Primicerio. This is an open-access article distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](#). The use, distribution and reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

Provisional

1 **The importance of ecological networks in multiple-stressor research**
2 **and management**

3

4 Andreas Bruder¹, André Frainer^{2,3*}, Thibault Rota⁴, Raul Primicerio³

5 ¹: Laboratory of Applied Microbiology, University of Applied Sciences and Arts of Southern
6 Switzerland, 6501 Bellinzona, Switzerland

7 ²: Norwegian Institute for Nature Research (NINA), Department of Arctic Ecology,
8 Framsenteret, 9296 Tromsø, Norway

9 ³: UiT The Arctic University of Norway, Faculty of Biosciences, Fisheries and Economics,
10 9037 Tromsø, Norway

11 ⁴: EcoLab, Université de Toulouse, CNRS, INP, UPS, 31062 Toulouse Cedex 9, France

12 *: corresponding author: andre.frainer@uit.no. UiT The Arctic University of Norway,
13 Faculty of Biosciences, Fisheries and Economics, 9037 Tromsø, Norway

14

15

16

17

18

19

20

21 Keywords: anthropogenic stressors, biotic communities, biotic interactions, ecosystem
22 restoration, food webs, statistical modelling, structural equation modelling.

23

24 **Summary**

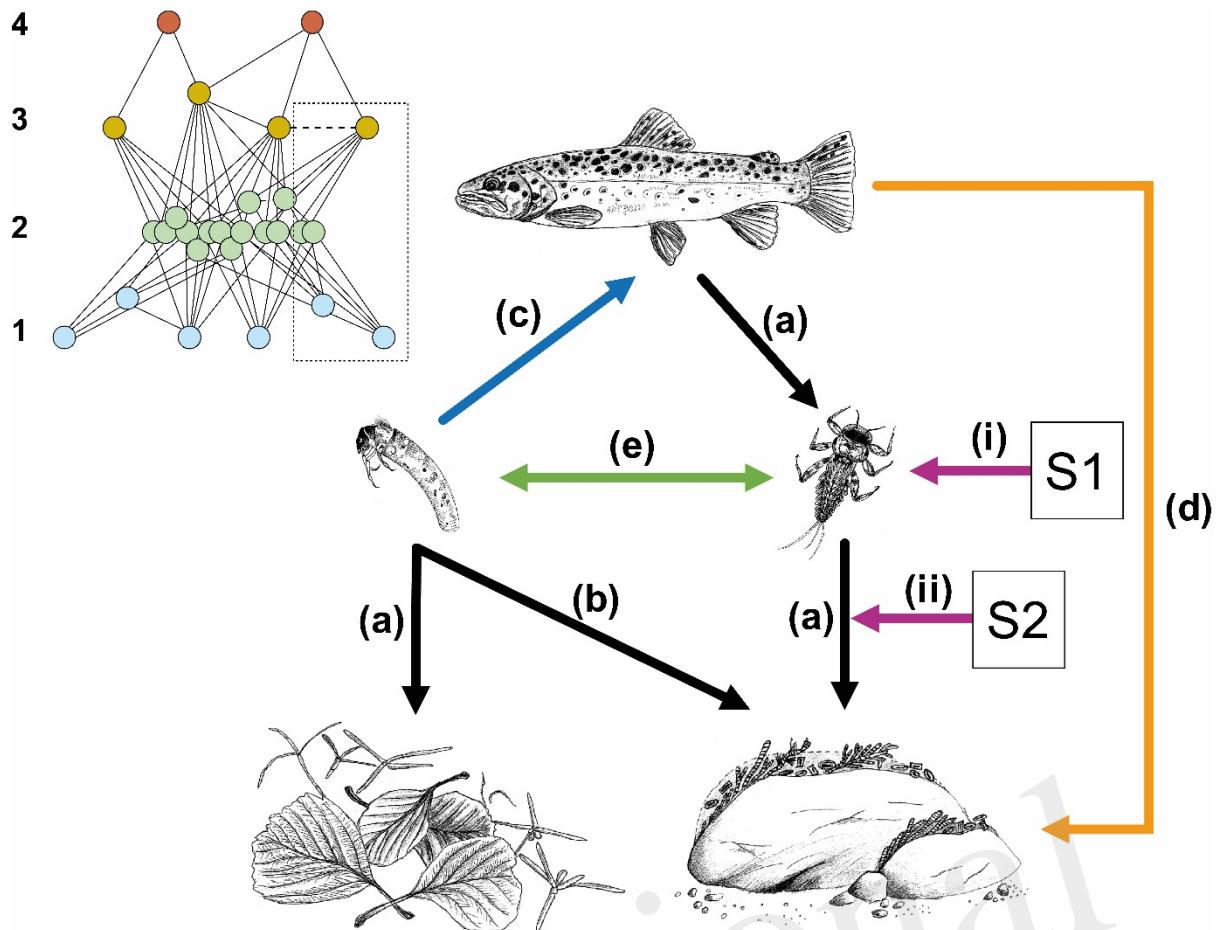
25 Multiple stressors are increasingly affecting organisms and communities, thereby modifying
26 ecosystems state and functioning. Raising awareness about the threat from multiple stressors
27 has increased the number of experimental and observational studies specifically addressing
28 consequences of stressor interactions on biota. Most studies measure the direct effects of
29 multiple stressors and their interactions on biological endpoints such as abundance, biomass,
30 or diversity of target organism groups. This yields invaluable information for the
31 management and restoration of stressed ecosystems. However, as we argue in our perspective
32 paper, this common approach ignores a fundamental characteristic of communities and
33 ecosystems, i.e. that organisms in ecosystems are interlinked by biotic interactions in
34 ecological networks. Examples from the literature show that biotic interactions can modify
35 stressor effects, transfer stressor effects to distant groups of organisms, and create new
36 stressor interactions. These examples also suggest that changes in biotic interactions can have
37 effects of similar or greater magnitude than direct stressor effects. We provide a perspective
38 on how to include network characteristics and biotic interactions into analyses of multiple-
39 stressor effects on ecosystems. A strength of our approach is that it can make use of
40 biomonitoring data produced with established and intercalibrated methods, and can combine
41 it with novel metrics used to describe the functioning of ecosystems, such as trait information
42 or stable-isotope measurements. The insights on network-mediated effects gained via the
43 approach we propose can substantially increase mechanistic understanding of multiple-
44 stressor effects, and in turn, the efficiency of ecosystem management and restoration.

45

46 **Introduction**

47 Anthropogenic stressors affecting organisms and ecosystems rarely occur in isolation.
48 Multiple stressors may interact in their effects on the biota, and complicate understanding and
49 assessment of anthropogenic impacts on ecosystems (Folt et al., 1999; Vinebrooke et al.,
50 2004), thus challenging ecosystem management and restoration (Côté et al., 2016). Global
51 sources of stressors, e.g. climate change, may interact with local stressors such as habitat loss,
52 invasive species, harvesting, and pollution, together affecting most ecosystems (e.g. Allan,
53 2004). Cumulative effects of multiple stressors on organisms, communities and ecosystems
54 are difficult to predict because exposure, sensitivity and adaptability to a given environmental
55 stressor are modified by the effects of other stressors (Vinebrooke et al., 2004). Awareness of
56 these challenges has markedly raised interest and activity in this research field in the last two
57 decades, thus slowly reducing the knowledge gap. Yet, one of the greatest challenges to
58 understand, assess and predict the impact of multiple stressors on communities and
59 ecosystems arises from stressor effects mediated and modified by biotic interactions
60 (Rosenblatt et al., 2017; Seibold et al., 2018).

61 Most multiple-stressor experiments and impact assessments focus on species or groups of
62 species as independent endpoints of analyses and correlate metrics describing them with
63 stressor intensities in univariate analyses. However, biotic interactions are relevant for multi-
64 stressed ecosystems because they mediate indirect effects of a stressor which can interact
65 with the direct or indirect effects of other stressors (Bruder et al., 2017; Schuwirth and
66 Reichert, 2013). Assessing biotic interactions is also indispensable for investigations of
67 ecosystem functioning in response to stressors (Gray et al., 2014), e.g. in the use as functional
68 indicators (Woodward et al., 2012). The intensity of biotic interactions is the result of
69 abundance, biomass, phenotype and behaviour of interacting species, which can all be
70 affected by stressors. Studies focusing on trophic interactions have revealed food-web
71 mediated effects of multiple stressors, but non-trophic interactions, such as facilitation and
72 competition (Brooks and Crowe, 2018), and pollinator-plant interactions (Raitif et al., 2019),
73 are also affected by multiple stressors with consequences at the ecosystem level. Accounting
74 for biotic interactions is also paramount to elucidate their role compared to that of
75 environmental factors (including stressors) and the interdependencies between the two in
76 shaping communities and ecosystems (Cadotte and Tucker, 2017; Schuwirth et al., 2016;
77 Seibold et al., 2018).



78

79 **Figure 1:** A simplified representation of biotic interactions in a stream food web based on leaf litter
80 (left-hand pathway) and periphyton (right-hand pathway) and affected by multiple stressors
81 (represented by stressors S1 and S2). Black arrows (a, b) represent trophic interactions with top-down
82 effects on resources, with (b) showing the use of a secondary resource by a consumer with a certain
83 degree of omnivory. The blue arrow (c) represents a trophic interaction with bottom-up effects on the
84 consumer. The orange arrow (d) represents an indirect consequence of trophic interactions, e.g.
85 cascading effects or trait-mediated effects, whereas the green arrow (e) represents non-trophic
86 interactions, e.g. competition/facilitation among species in the same trophic level. Purple arrows
87 represent multiple stressors (S1 and S2) with effects on organism groups (i) and on interactions (ii),
88 e.g. due to changes in foraging activity. The inset shows the complete network of species at the site of
89 which the large scheme is an extract or simplification as shown by the dotted box. Blue nodes in the
90 inset represent basal resources (including autotroph and heterotroph microorganisms, e.g. fungi;
91 trophic level 1), green nodes represent invertebrates (trophic level 2), and orange (trophic level 3) and
92 red nodes (trophic level 4) represent fish. Trophic interactions in the network are exemplified by
93 continuous lines and non-trophic interactions by the dashed lines.

94

95 Species in communities are connected via a network of biotic interactions – both trophic and
96 non-trophic interactions (Fig. 1) – which as a whole determine ecosystem vulnerability and
97 functioning with implications for management (Harvey et al., 2017; Seibold et al., 2018;
98 Tylianakis et al., 2010). The impact of the multiple stressors on communities and ecosystems
99 depends on the structure of ecological networks and the positions and roles of affected
100 species therein (Table 1; Montoya et al., 2006). Network characteristics such as connectance
101 (i.e. the proportion of realized out of all possible interactions) and modularity (degree to
102 which species form distinct clusters of tightly interacting nodes) are relevant for network
103 stability, and the impacts and spread of stressor effects (Kortsch et al., 2015). Quantifying
104 and testing these and other network characteristics (Gray et al., 2014; Lau et al., 2017) in
105 addition to specific biotic interactions may thus yield crucial information about impact of and
106 vulnerability to multiple stressors not only for the parts (e.g. species and biotic interactions),
107 but for the ecosystem as a whole.

108

109 **Table 1:** Examples of network characteristics (a), and characteristics of species in networks (b), and
 110 their attributes relevant for stressor effects. These characteristics may either change due to stressors or
 111 may infer resistance to stressors. Changes in these characteristics manifest in changes of abundance,
 112 biomass, and diversity of organisms groups, or ecosystem processes, i.e. metrics commonly measured
 113 in multiple-stressor experiments and biomonitoring. See Lau et al. (2017) for an overview on network
 114 characteristics and on modelling approaches for their analysis.

a) Network characteristic	Definition	Relevance for stressor effects	References
Connectance	Proportion of realized interactions out of all possible interactions	Resistance and resilience to perturbations	[1], [2]
Distribution of interaction strength	Frequency distribution of interaction strength, identity of strong interactions	Fluxes of energy and nutrients	[2], [3], [4]
Modularity	Degree to which species form distinct clusters of tightly interacting nodes	Resistance to perturbations; Fluxes of energy and nutrients	[1], [4]
Diversity	Species richness, functional diversity	Adaptive capacity and resistance to perturbations	[5], [6], [7], [8], [9], [10], [11]
Food-chain length	Number of species directly connected by trophic links from top predators to basal resources	Biomagnification of pollutants	[12]

b) Species characteristics	Definition	Relevance for stressor effects	References
Trophic position	Trophic position in the food web	Cascading effects	[1], [13]
Omnivory	Resource use across trophic levels	Fluxes of energy and nutrients	[1], [4]

[1] Kortsch et al. (2015), [2] Tylianakis et al. (2007), [3] Bruder et al. (2017), [4] Schrama et al. (2017), [5] Alexander et al. (2016), [6] Bakker et al. (2013), [7] Bentivoglio et al. (2016), [8] Brittain and Strecker (2018), [9] Frainer and McKie (2015), [10] Schuwirth et al. (2016), [11] Gardeström et al. (2016), [12] Borgå et al. (2001), [13] Fu et al. (2018).

115

116 Statistical approaches to simultaneously quantify direct and indirect stressor effects as well as
 117 biotic interactions in complex communities and food webs have been developed and applied
 118 in multiple-stressor studies. Among them, structural equation modelling (SEM; Grace, 2006;
 119 Grace et al., 2010) is a powerful approach to investigate effects mediated by complex causal
 120 structures, and to test the direction and magnitude of the relationships specified by
 121 hypothesized causal links between multiple stressors and interacting species (see also
 122 Supplementary Material). SEM may thus yield valuable mechanistic understanding of
 123 multiple-stressor effects in ecological networks and communities (Grace et al., 2016). Other
 124 empirical modelling tools that efficiently address the combined effects of multiple stressors
 125 and biotic interactions include state-space models, appropriate when time-series data is
 126 available (Tett et al., 2013), and ecological network analyses (reviewed in Lau et al., 2017),

127 which allow to address whole ecosystem responses for highly resolved food webs (Fu et al.,
128 2018). Mechanistic models have also proven useful in analysing data from observational
129 multiple-stressor studies (Schuwirth et al., 2016). We believe that embracing ecological
130 network theory and using statistical approaches that allow testing and quantifying effects
131 mediated by biotic interactions and network characteristics would greatly benefit research
132 and management of communities and ecosystems exposed to multiple stressors.

133 **Applications of the network perspective in multiple-stressor research**

134 Biotic interactions addressed in multiple-stressor studies may span from two-species systems
135 to entire communities containing hundreds of species. System simplifications is often
136 required in experimental studies (Fig. 1, discussed below) and might lead to more robust
137 analyses of direct and indirect causal pathways, whereas assessments of complete ecological
138 networks might yield crucial understanding of ecosystem-level perturbations (Fig. 1 inset).
139 Here, we illustrate how biotic interactions might be included in multiple-stressors studies on
140 two scales of complexity, (i) on simplifications of the network aiming at resolving causal
141 pathways and measuring processes in detail, and (ii) on assessments of complex food-web
142 interactions aimed at analysing energy pathways and network characteristics.

143 ***Experimental studies of food-web mediated stressor effects***

144 Field experiments yield important insights into how multiple stressors may affect real
145 ecosystems. Working on a land-use gradient in boreal streams, Frainer and McKie (2015)
146 analysed how land use affects the detritivorous invertebrate community and leaf litter
147 decomposition rates. Their SEM analyses revealed indirect effects of agricultural stressors on
148 decomposition rates of birch litter (*Betula pendula*) mediated by changes in the density,
149 functional composition and functional diversity of the invertebrate community. Their results
150 also indicated that indirect stressor effects had similar magnitudes as direct effects. Schuwirth
151 et al. (2016) tested the effects of agricultural and urban stressors on invertebrate communities
152 using a mechanistic model based on Bayesian inference (Schuwirth and Reichert, 2013) and
153 found that biotic interactions among invertebrate taxa (i.e. trophic interactions and
154 competition) were more important in explaining their occurrence at a given site than their
155 sensitivity to stressors.

156 The above examples are from field assessments, but experiments in mesocosms are
157 increasingly used to test responses of communities to multiple stressors as they represent a
158 useful compromise between experimental control and ecological realism (Stewart et al.,

159 2013). Bruder et al. (2017) tested the effects of agricultural stressors on stream food webs in
160 flow-through mesocosms. In their experiment, SEM revealed an indirect negative effect of
161 reduced flow on the condition of juvenile brown trout (*Salmo trutta*) by lowering the
162 abundance of invertebrate prey. This effect interacted synergistically with raising water
163 temperatures (a direct stressor) in increasing fish mortality. In a similar experiment,
164 Rodrigues et al. (2018) used SEM to quantify direct and indirect effects of an insecticide and
165 of invasive species on a stream food web. In their study, indirect effects explained positive
166 effects of an invasive top-predator (Louisiana crayfish, *Procambarus clarkii*) on algal growth
167 and a positive effect of the insecticide on invertebrate prey survival due to behavioural
168 changes, which reduced cues used by the predator.

169 Also in mesocosms, Alexander et al. (2013) tested the interactions between an insecticide-
170 mixture, nutrient levels and predator identity on a stream food web. Using SEM, they found
171 that insecticide stress resulted in a significant cascading effect on invertebrate abundance of
172 lower trophic levels by alleviating the effect of a stonefly predator (*Agnetina* spp.).
173 Interestingly, this top-down link was not detected in nutrient enriched treatments, possibly
174 because it was masked by a positive effect of nutrients on biofilm-associated resources for the
175 invertebrate community (i.e. a bottom-up link). In mesocosms mimicking agricultural ditches,
176 Schrama et al. (2017) studied the effects of nutrients and insecticides on resource use by
177 invertebrates using stable-isotope analysis. They found that grazers and detritivores
178 preferentially fed on animal remains in stressed conditions, which became more available due
179 to increased mortality, resulting in shifts in resource use, trophic position, and food-chain
180 length.

181 ***Energy pathway and network analyses***

182 Studies may analyse how network characteristics of food webs change due to multiple
183 stressors. For example, O’Gorman et al. (2012) analysed how intertidal communities are
184 affected by the addition of nitrogen and organic matter. Using generalized linear models
185 (GLM) they found that the two stressors had additive effects on food-web connectance and
186 mean food-chain length. Using a highly resolved food web with 180 trophospecies and 1546
187 trophic links, Kortsch et al. (2015) analysed how the addition of four generalist boreal fish
188 species, which are moving into the Arctic due to climate-driven poleward migration, affect
189 the structure of Arctic marine food webs. Their analyses revealed that the incoming species
190 increased connectance and reduced modularity, resulting in a stronger benthic-pelagic link in
191 the Arctic food web. Finally, Fu et al. (2018) utilized four different ecosystem models,

192 including Ecopath with Ecosim (Christensen and Walters, 2004) and Atlantis (Fulton et al.,
193 2004), to assess how fishing and primary productivity affect marine food webs in various
194 regions around the globe. They found that taxa from lower trophic levels were more
195 negatively affected by the combined pressure of fishing and low productivity (i.e.
196 phytoplankton biomass) than those from higher trophic levels.

197 **Discussion**

198 Integrating a network perspective and biotic interactions into the analysis of multiple-stressor
199 experiments or impact assessments provides crucial information on stressor effects on
200 organisms, communities and ecosystem processes, and on their vulnerability to further
201 environmental change. Testing biotic interactions explicitly may elucidate indirect stressor
202 effects, which seem common in most ecosystem types given the complexity of their
203 ecological network (Harvey et al., 2017). Accounting for biotic interactions and network
204 characteristics may also yield important mechanistic information on the stressors' mode of
205 action. The perspective we propose provides a foundation for simultaneous quantitative
206 estimates of alterations in taxonomic and functional community composition due to multiple
207 stressors and their consequences on ecosystem functioning (Fig. 1). Excluding these
208 fundamental characteristics of biotic communities may thus limit the interpretation and
209 applicability of findings from multiple-stressor analyses to research and management (see
210 also Gray et al., 2014).

211 Indirect stressor effects mediated by biotic interactions are particularly relevant in a multiple-
212 stressor context given the potential of stressors to ripple through communities and ecological
213 networks, resulting in stressors interactions at distant organism groups (see examples above).
214 Stressors change the availability of basal resources, consumer biomass, and behavioural or
215 morphological traits, all affecting the intensity of consumption and energy flows (Alexander
216 et al., 2016; Brodin et al., 2014; Rodrigues et al., 2018). Stressors may also increase
217 susceptibility to infectious organisms (e.g. parasites; Hofmann et al., 2016; Studer and
218 Poulin, 2013), with potential knock-on effects on host phenotype and ecological processes
219 (Frainer et al. 2018). Indirect stressor effects mediated by biotic interactions may then
220 interact with the effects of direct stressors and/or other indirect stressors near the top (Bruder
221 et al., 2017) and the bottom of food webs (Alexander et al., 2016).

222 Biotic interactions also underlie masking effects that might occur when measuring species as
223 independent endpoints of the analysis. Masking effects may be based on adaptation in

resource use by consumers when measuring their biomass (Alexander et al., 2013), functional redundancy of consumers when measuring resource use (Rodrigues et al., 2018), or cascading effects across more than two trophic levels (Alexander et al., 2013; Rodrigues et al., 2018). Masking may erroneously be interpreted as organisms being insensitive or resistant towards the stressors. The above examples involve trophic interactions but indirect stressor effects may also be caused by non-trophic interactions. These may occur if stressors cause functional or density changes in organisms, thus triggering trait or density-mediated alterations of non-trophic interactions, e.g. competition and facilitation (Brooks and Crowe, 2018; Clements et al., 1989; Rodrigues et al., 2018). Specifically testing biotic interactions can reveal such indirect stressor effects, novel stressor combinations, and their ecosystem-level consequences.

Consequences of multiple stressors mediated by biotic interactions can alter network characteristics of communities due to changes in density, biomass, and/or traits of component species (Table 1; Lau et al., 2017). Stressor effects may manifest for instance as changes to network stability and its response to additional stressors, all potentially affecting overall resource use, flux of energy and nutrients and other ecosystem processes (Fu et al., 2018; Kortsch et al., 2015). In many cases, the data available from experimental and observational studies, impact assessments, and ecosystem management is insufficient to test all network characteristics (Tylianakis et al., 2010). Knowledge on interactions among all taxa would be required (e.g. on trophic links established through gut-content or stable-isotope analyses; Gray et al., 2014; Schuwirth et al., 2016), which is challenging because the number of potential interactions and stressor impacts increases exponentially with taxon richness (Lau et al., 2017; Tylianakis et al., 2010). Interestingly, estimates of connectance seem to saturate more rapidly with sampling effort than most other network characteristics (Tylianakis et al., 2010) and may provide a good starting point.

Whichever the most appropriate approach for data analysis, reductions of the biological complexity of networks will often be required (Fig. 1; Frainer et al., 2017; Schuwirth and Reichert, 2013). Possibilities include simplifying networks to few key taxa and species interactions that are carefully quantified (Bruder et al., 2017; Gardeström et al., 2016; Schrama et al., 2017), pooling species into higher-order taxa, feeding guilds or other functional attributes (Fu et al., 2018; Schrama et al., 2017; Schuwirth et al., 2016), or characterizing species in a multivariate space and utilizing one or few dimensions of that space as the variable(s) describing the community (Frainer and McKie, 2015). Obviously,

257 such reductions have to be done with caution and sufficient knowledge of the study system in
258 order to avoid oversimplification. Nevertheless, if done correctly, these simplifications
259 represent attractive compromises between data availability and testing of relevant ecological
260 questions.

261 Stressor effects may modify biotic interactions and network characteristics of communities in
262 multi-stressed ecosystems and are thus relevant for biomonitoring (Gray et al., 2014) and
263 ecosystem management (Carvalho et al., 2019), but also for ecotoxicology (Clements and
264 Rohr, 2010; Nilsen et al., 2019; Preston, 2002; Segner et al., 2014). Although our examples
265 are mainly derived from aquatic ecosystems, the findings and concepts we present are
266 founded on ecological theory and thus transferable to most other ecosystems, as exemplified
267 by similar studies in grasslands (Grace et al., 2016) and urban soils (Tresch et al., 2019). The
268 perspective and approaches we propose have the potential to yield ecologically more
269 complete findings and in turn to increase the benefit from the resources invested in ecosystem
270 assessment and management.

271 **Acknowledgements**

272 We greatly appreciate the invitation of the Editors of the Frontiers special issue on “Multiple
273 stressors across ecosystem boundaries” to contribute this perspective paper. We are also
274 grateful for the comments by R. A. Paterson, K. Lange and two anonymous reviewers on
275 earlier versions of the manuscript. Funding for publication fees was granted by the
276 publication fund of UiT The Arctic University of Norway.

277 **Bibliography**

- 278 Alexander, A. C., Culp, J. M., Baird, D. J., and Cessna, A. J. (2016). Nutrient–insecticide
279 interactions decouple density-dependent predation pressure in aquatic insects. *Freshw.*
280 *Biol.* 61, 2090–2101. doi:10.1111/fwb.12711.
- 281 Alexander, A. C., Luis, A. T., Culp, J. M., Baird, D. J., and Cessna, A. J. (2013). Can
282 nutrients mask community responses to insecticide mixtures? *Ecotoxicology* 22, 1085–
283 1100. doi:10.1007/s10646-013-1096-3.
- 284 Allan, J. D. (2004). Landscapes and riverscapes: the influence of land use on stream
285 ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 35, 257–284.
286 doi:10.1146/annurev.ecolsys.35.120202.110122.
- 287 Bakker, E. S., Dobrescu, I., Straile, D., and Holmgren, M. (2013). Testing the stress gradient
288 hypothesis in herbivore communities: facilitation peaks at intermediate nutrient levels.

- 289 *Ecology* 94, 1776–1784. doi:10.1890/12-1175.1.
- 290 Bentivoglio, F., Calizza, E., Rossi, D., Carlino, P., Careddu, G., Rossi, L., et al. (2016). Site-
291 scale isotopic variations along a river course help localize drainage basin influence on
292 river food webs. *Hydrobiologia* 770, 257–272. doi:10.1007/s10750-015-2597-2.
- 293 Borgå, K., Gabrielsen, G. W., and Skaare, J. U. (2001). Biomagnification of organochlorines
294 along a Barents Sea food chain. *Environ. Pollut.* 113, 187–198. doi:10.1016/S0269-
295 7491(00)00171-8.
- 296 Brittain, J. T., and Strecker, A. L. (2018). The interactive effect of multiple stressors on
297 crustacean zooplankton communities in montane lakes. *Water Resour. Res.* 54, 939–954.
298 doi:10.1002/2017WR020605.
- 299 Brodin, T., Piovano, S., Fick, J., Klaminder, J., Heynen, M., and Jonsson, M. (2014).
300 Ecological effects of pharmaceuticals in aquatic systems—impacts through behavioural
301 alterations. *Philos. Trans. R. Soc. B Biol. Sci.* 369, 20130580.
302 doi:10.1098/rstb.2013.0580.
- 303 Brooks, P. R., and Crowe, T. P. (2018). Density and biotic interactions modify the combined
304 effects of global and local stressors. *Oikos* 127, 1746–1758. doi:10.1111/oik.04459.
- 305 Bruder, A., Salis, R. K., Jones, P. E., and Matthaei, C. D. (2017). Biotic interactions modify
306 multiple-stressor effects on juvenile brown trout in an experimental stream food web.
307 *Glob. Chang. Biol.* 23, 3882–3894. doi:10.1111/gcb.13696.
- 308 Cadotte, M. W., and Tucker, C. M. (2017). Should environmental filtering be abandoned?
309 *Trends Ecol. Evol.* 32, 429–437. doi:10.1016/j.tree.2017.03.004.
- 310 Carvalho, L., Mackay, E. B., Cardoso, A. C., Baattrup-Pedersen, A., Birk, S., Blackstock, K.
311 L., et al. (2019). Protecting and restoring Europe’s waters: An analysis of the future
312 development needs of the Water Framework Directive. *Sci. Total Environ.* 658, 1228–
313 1238. doi:10.1016/j.scitotenv.2018.12.255.
- 314 Christensen, V., and Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and
315 limitations. *Ecol. Modell.* 172, 109–139. doi:10.1016/j.ecolmodel.2003.09.003.
- 316 Clements, W. H., Cherry, D. S., and Cairns, J. J. (1989). The influence of copper exposure on
317 predator-prey interactions in aquatic insect communities. *Freshw. Biol.* 21, 483–488.
318 doi:10.1111/j.1365-2427.1989.tb01381.x.
- 319 Clements, W. H., and Rohr, J. R. (2010). Community responses to contaminants: Using basic
320 ecological principles to predict ecotoxicological effects. *Environ. Toxicol. Chem.* 28,

- 321 1789–1800. doi:10.1897/09-140.1.
- 322 Côté, I. M., Darling, E. S., and Brown, C. J. (2016). Interactions among ecosystem stressors
323 and their importance in conservation. *Proc. R. Soc. B Biol. Sci.* 283. doi:
324 10.1098/rspb.2015.2592.
- 325 Folt, C. L., Chen, C. Y., Moore, M. V., and Burnaford, J. (1999). Synergism and antagonism
326 among multiple stressors. *Limnol. Oceanogr.* 44, 864–877. doi:
327 10.4319/lo.1999.44.3_part_2.0864.
- 328 Trainer, A., and McKie, B. G. (2015). Shifts in the diversity and composition of consumer
329 traits constrain the effects of land use on stream ecosystem functioning. *Adv. Ecol. Res.*
330 52, 169–200. doi:10.1016/bs.aecr.2015.03.002.
- 331 Trainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., et al. (2017).
332 Climate-driven changes in functional biogeography of Arctic marine fish communities.
333 *Proc. Natl. Acad. Sci.* 114, 12202 LP-12207. doi:10.1073/pnas.1706080114.
- 334 Fu, C., Travers-Trolet, M., Velez, L., Grüss, A., Bundy, A., Shannon, L. J., et al. (2018).
335 Risky business: The combined effects of fishing and changes in primary productivity on
336 fish communities. *Ecol. Modell.* 368, 265–276. doi:10.1016/j.ecolmodel.2017.12.003.
- 337 Fulton, E. A., Parslow, J. S., Smith, A. D. M., and Johnson, C. R. (2004). Biogeochemical
338 marine ecosystem models II: the effect of physiological detail on model performance.
339 *Ecol. Modell.* 173, 371–406. doi:10.1016/j.ecolmodel.2003.09.024.
- 340 Gardeström, J., Ermold, M., Goedkoop, W., and McKie, B. G. (2016). Disturbance history
341 influences stressor impacts: effects of a fungicide and nutrients on microbial diversity
342 and litter decomposition. *Freshw. Biol.* 61, 2171–2184. doi:10.1111/fwb.12698.
- 343 Grace, J. (2006). *Structural equation modeling and natural systems*. New York, NY, USA:
344 Cambridge University Press.
- 345 Grace, J. B., Anderson, T. M., Olff, H., and Scheiner, S. M. (2010). On the specification of
346 structural equation models for ecological systems. *Ecol. Monogr.* 80, 67–87.
347 doi:10.1890/09-0464.1.
- 348 Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., et
349 al. (2016). Integrative modelling reveals mechanisms linking productivity and plant
350 species richness. *Nature* 529, 390. doi:10.1038/nature16524.
- 351 Gray, C., Baird, D. J., Baumgartner, S., Jacob, U., Jenkins, G. B., O’Gorman, E. J., et al.
352 (2014). FORUM: Ecological networks: the missing links in biomonitoring science. *J.*

- 353 *Appl. Ecol.* 51, 1444–1449. doi:10.1111/1365-2664.12300.

354 Harvey, E., Gounand, I., Ward, C. L., and Altermatt, F. (2017). Bridging ecology and
355 conservation: from ecological networks to ecosystem function. *J. Appl. Ecol.* 54, 371–
356 379. doi:10.1111/1365-2664.12769.

357 Hofmann, H., Blasco-Costa, I., Knudsen, R., Matthaei, C. D., Valois, A., and Lange, K.
358 (2016). Parasite prevalence in an intermediate snail host is subject to multiple
359 anthropogenic stressors in a New Zealand river system. *Ecol. Indic.* 60, 845–852.
360 doi:10.1016/j.ecolind.2015.08.022.

361 Kortsch, S., Primicerio, R., Fossheim, R., Dolgov, A. V., and Aschan, M. (2015). Climate
362 change alters the structure of arctic marine food webs due to poleward shifts of boreal
363 generalists. *Proc. R. Soc. B Biol. Sci.* 282, 20151546. doi:10.1098/rspb.2015.1546.

364 Lau, M. K., Borrett, S. R., Baiser, B., Gotelli, N. J., and Ellison, A. M. (2017). Ecological
365 network metrics: Opportunities for synthesis. *Ecosphere* 8, e01900.
366 doi:10.1002/ecs2.1900.

367 Montoya, J. M., Pimm, S. L., and Solé, R. V (2006). Ecological networks and their fragility.
368 *Nature* 442, 259–264. doi:10.1038/nature04927.

369 Nilsen, E., Smalling, K. L., Ahrens, L., Gros, M., Miglioranza, K. S. B., Pico, Y., et al.
370 (2019). Critical review: Grand challenges in assessing the adverse effects of
371 contaminants of emerging concern on aquatic food webs. *Environ. Toxicol. Chem.* 38,
372 46–60. doi:10.1002/etc.4290.

373 O’Gorman, E. J., Fitch, J. E., and Crowe, T. P. (2012). Multiple anthropogenic stressors and
374 the structural properties of food webs. *Ecology* 93, 441–448. doi:10.1890/11-0982.1.

375 Preston, B. L. (2002). Indirect effects in aquatic ecotoxicology: implications for ecological
376 risk assessment. *Environ. Manage.* 29, 311–323. doi:10.1007/s00267-001-0023-1.

377 Raitif, J., Plantegenest, M., and Roussel, J.-M. (2019). From stream to land: Ecosystem
378 services provided by stream insects to agriculture. *Agric. Ecosyst. Environ.* 270–271,
379 32–40. doi:10.1016/j.agee.2018.10.013.

380 Rodrigues, A. C. M., Machado, A. L., Bordalo, M. D., Saro, L., Simão, F. C. P., Rocha, R. J.
381 M., et al. (2018). Invasive species mediate insecticide effects on community and
382 ecosystem functioning. *Environ. Sci. Technol.* 52, 4889–4900.
383 doi:10.1021/acs.est.8b00193.

384 Rosenblatt, A. E., Smith-Ramesh, L. M., and Schmitz, O. J. (2017). Interactive effects of

- 385 multiple climate change variables on food web dynamics: Modeling the effects of
386 changing temperature, CO₂, and water availability on a tri-trophic food web. *Food Webs*
387 13, 98–108. doi:10.1016/j.fooweb.2016.10.002.
- 388 Schrama, M., Barmentlo, S. H., Hunting, E. R., van Logtestijn, R. S. P., Vijver, M. G., and
389 van Bodegom, P. M. (2017). Pressure-induced shifts in trophic linkages in a simplified
390 aquatic food web. *Front. Environ. Sci.* 5, 75. doi:10.3389/fenvs.2017.00075.
- 391 Schuwirth, N., Dietzel, A., and Reichert, P. (2016). The importance of biotic interactions for
392 the prediction of macroinvertebrate communities under multiple stressors. *Funct. Ecol.*
393 30, 974–984. doi:10.1111/1365-2435.12605.
- 394 Schuwirth, N., and Reichert, P. (2013). Bridging the gap between theoretical ecology and real
395 ecosystems: modeling invertebrate community composition in streams. *Ecology* 94,
396 368–379. doi:10.1890/12-0591.1.
- 397 Segner, H., Schmitt-Jansen, M., and Sabater, S. (2014). Assessing the impact of multiple
398 stressors on aquatic biota: the receptor's side matters. *Environ. Sci. Technol.* 48, 7690–
399 7696. doi:10.1021/es405082t.
- 400 Seibold, S., Cadotte, M. W., MacIvor, J. S., Thorn, S., and Müller, J. (2018). The necessity of
401 multitrophic approaches in community ecology. *Trends Ecol. Evol.*
402 doi:10.1016/j.tree.2018.07.001.
- 403 Stewart, R. I. A., Dossena, M., Bohan, D. A., Jeppesen, E., Kordas, R. L., Ledger, M. E., et
404 al. (2013). Mesocosm experiments as a tool for ecological climate-change research. *Adv.
405 Ecol. Res.* 48. doi:10.1016/B978-0-12-417199-2.00002-1.
- 406 Studer, A., and Poulin, R. (2013). Cercarial survival in an intertidal trematode: a
407 multifactorial experiment with temperature, salinity and ultraviolet radiation. *Parasitol.
408 Res.* 112, 243–249. doi:10.1007/s00436-012-3131-3.
- 409 Tett, P., Gowen, R., Painting, S., Elliott, M., Forster, R., Mills, D., et al. (2013). Framework
410 for understanding marine ecosystem health. *Mar. Ecol. Prog. Ser.* 494, 1–27.
411 doi:10.3354/meps10539.
- 412 Tresch, S., Frey, D., Le Bayon, R.-C., Zanetta, A., Rasche, F., Fliessbach, A., et al. (2019).
413 Litter decomposition driven by soil fauna, plant diversity and soil management in urban
414 gardens. *Sci. Total Environ.* 658, 1614–1629. doi:10.1016/j.scitotenv.2018.12.235.
- 415 Tylianakis, J. M., Laliberté, E., Nielsen, A., and Bascompte, J. (2010). Conservation of
416 species interaction networks. *Biol. Conserv.* 143, 2270–2279.

- 417 doi:10.1016/j.biocon.2009.12.004.
- 418 Tylianakis, J. M., Tscharntke, T., and Lewis, O. T. (2007). Habitat modification alters the
419 structure of tropical host-parasitoid food webs. *Nature* 445, 202-205.
420 doi:10.1038/nature05429.
- 421 Vinebrooke, R. D., Cottingham, K. L., Norberg, M. S., Dodson, S. I., Maberly, S. C.,
422 Sommer, U., et al. (2004). Impacts of multiple stressors on biodiversity and ecosystem
423 functioning: The role of species co-tolerance. *Oikos* 104, 451–457. doi:10.1111/j.0030-
424 1299.2004.13255.x.
- 425 Woodward, G., Gessner, M. O., Giller, P. S., Gulis, V., Hladyz, S., Lecerf, A., et al. (2012).
426 Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science*
427 336, 1438–1440. doi:10.1126/science.1219534.
- 428

Figure 01.JPG

