How species respond to changes in environmental variability has been shown for single species, but the question remains whether these results are transferable to species when incorporated in ecological communities. Here, we address this issue by analysing the same species exposed to a range of environmental variabilities when (i) isolated or (ii) embedded in a food web. We find that all species in food webs exposed to temporally uncorrelated environments (white noise) show the same type of dynamics as isolated species, whereas species in food webs exposed to positively autocorrelated environments (red noise) can respond completely differently compared with isolated species. This is owing to species following their equilibrium densities in a positively autocorrelated environment that in turn enables species–species interactions to come into play. Our results give new insights into species’ response to environmental variation. They especially highlight the importance of considering both species’ interactions and environmental autocorrelation when studying population dynamics in a fluctuating environment.

1. Introduction

Ecosystems are exposed to environmental conditions that vary through time owing to natural- or human-induced reasons. Understanding how the populations in ecosystems respond to these fluctuations is of major importance for ecology, especially given ongoing changes in the mean and variability of climate conditions [1]. Both empirical and theoretical work suggests that the pattern of species–species interactions will affect species’ response to environmental variation [2–6]. Thus, single species studies may misinform us as we know that species are not isolated but rather form complex networks of interactions [4,7–9]. However, what factor is the main driver of observed population dynamics—environmental variation or species–species interactions—is still an open question. If environmental conditions are the main driver, we expect a similar environmental response between single species and species embedded in food webs. If instead the species–species interactions are prevalent, there ought to be an inconsistency between the two responses.

Species can respond to their environmental conditions in various ways [10]. One example that highlights this diversity of species’ responses is the work of Morris et al. [11], who analysed multiyear demographic data for different plants and animals. They found that all species were affected by environmental variability, but also that the response greatly differed between species. Population growth rate is one factor that can cause differences in species’ environmental response within food webs [12]. Additionally, multiple studies on food web models have revealed the potential for both large [13,14] as well as small [15] changes in species’ densities or structural changes [16,17] to give cascading effects on other positions in the food web. The combined effect from environmental variation and species–species interactions is likely complex but nevertheless utterly important to disentangle.

The variability of environmental conditions over time can be described by the variance and autocorrelation of the environmental time series [18]. Climate
change is expected to affect both of these factors [1,19–21]. The work presented here focuses on environmental autocorrelation, which is referred to as the colour of time series. White time series have no autocorrelation, i.e. a value at one time step is not dependent on the values in previous time steps. Red time series, on the other hand, have positive autocorrelation, i.e. a value at a specific time is similar to ones in preceding time steps, giving a slower change over time in comparison to white time series.

Time series of temperature, precipitation and other environmental variables show different degrees of redness [22]. Terrestrial environments are expected to have a redness between white and red (pink), whereas marine environments often have red or even darker red colour [22–25]. Time series of population densities are also usually red [26,27] but the degree of redness can differ between taxa [19] as well as between species in aquatic and terrestrial environments [28,29]. Population dynamics in food webs are often red-denied without the forcing of environmental variation owing to density dependence [19]. Red time series of species’ densities have the potential to interact, or resonate, with red environmental variation if their periods coincide [30]. Red environmental variation may thereby reveal differences between the environmental response of single species and species in food webs.

The first theoretical studies on how environmental autocorrelation affects population dynamics were done on single species models where a species’ response was described by analysing how well the populations track the environmental conditions [31,32]. The degree of tracking was measured by tracking error (TE), a measure of how a population density follows the fluctuations in its environmental conditions. In the single species case, TE decreases with increased redness in environmental conditions. Population densities follow the fluctuations in red environmental variation more closely than white since the change over time then is slower. Consequently, single species’ population variance will increase with increasing environmental redness until population variance resembles that of the environmental conditions. In this, the pattern results in decreased population stability (defined as 1/CV, where CV is the coefficient of variation—population standard deviation divided by population mean), with increased redness in the environmental variation [31,32].

More recent studies have shown that single species with time-lags in their density dependence (e.g. discrete models with overcompensating dynamics) may respond differently [27,33,34]. Population stability will initially increase with increased environmental redness, reach a maximum and then start to decrease with further increase in environmental redness. This type of response depends on population densities that overshoot their equilibrium when environmental conditions change fast in comparison with the population dynamics. The responses of species in food web models to environmental redness have been proved to be highly dependent on factors such as; species’ dynamical speed [35], environmental sensitivity of species’ equilibria [36] and the synchrony of species’ environmental responses [37,38]. Even though the response to increased environmental redness is quite straightforward for single species models, there is no consensus on how we should extend that knowledge when the same species is embedded in a food web.

To address this knowledge gap, we analysed the difference in a population’s response to changed environmental autocorrelation between single species and species in food web models. We used food web models with a range of different sizes, structures and parameter set-ups. In order to compare our results with prior single species theory, we studied each resource species in each food web when: (i) acting as a single species and (ii) interacting with the other species in its food web. We found that while some species in food webs respond in the same way as their single species counterpart, others respond in an opposite manner. This pattern can be explained by combining classical single species results with theory of species–species interactions within food webs.

2. Material and method

(a) Food web models

We consider eight food web models with different structures and three trophic levels: resource, consumer and predator species (figure 1). The food web models have three to six species and include the basic types of trophic interrelationships such as apparent competition, omnivory and intraguild predation. Together, they represent a gradual shift from simple food chains to more complex food webs with multiple consumers, intraguild predation and interspecific competition.

Figure 1. The eight different food web models studied were: M1, a diamond-shaped food web with the top predator feeding on two intermediate consumers (apparent competition); M2, a triangular-shaped food web with a diamond-shaped core; M3, a triangular-shaped food web including omnivory and species–species competition between resources; M4, a food web with consumer one feeding on the resource and on the second consumer (intraguild predation); M5, a triangular-shaped food web including intraguild predation; M6, a food web with multiple resources, species–species competition between resources and omnivory; M7, a food chain with two resources, M8, a simple food chain with omnivory. Designations: P, the top predator; C, the consumer; and R, the resource species. The grey gradient denotes a gradual shift in food web complexity from simple food chains to more complex food webs with multiple consumers, intraguild predation and interspecific competition.
per capita growth (mortality) rate for resource (consumer and predator) species \( i \), and \( \tilde{a}_i \) is the per capita effect of species \( j \) on the per capita growth rate of species \( i \). Consumption is limited by a type II functional response in which:

\[
\begin{align*}
\tilde{a}_i &= a_i / K_i, \\
\tilde{a}_i &= -J_i \hat{\Omega}_{ij} / (H_i + T \sum_{j \in \text{set}} J_i \hat{\Omega}_{ij}N_j), \quad j \in C(i), \\
\tilde{a}_i &= J_i \hat{\Omega}_{ij} / (H_i + T \sum_{j \in \text{set}} J_i \hat{\Omega}_{ij}N_j), \quad j \in R(i),
\end{align*}
\]

where \( L(i) \) contains species of the same trophic level as species \( i \), \( C(i) \) contains species that consume species \( i \), and \( R(i) \) contains species that species \( i \) consume. \( a_i \) is the species–species competition (defined as \( r_i \tilde{d}_i / K_i \), where \( K_i \) is the carrying capacity of species \( i \)), \( J_i \) is species \( j \)’s ingestion rate of species \( i \), \( \Omega_{ij} \) is the preference coefficient of predator \( j \) on prey \( i \), \( H_i \) is the half saturation constant of species \( i \), \( T \) is the handling time of prey, and \( e \) is the conversion efficiency.

For each food web model, we generated replicate food webs with parameters sampled from a predefined parameter distribution (electronic supplementary material, table S2–S4). The algorithm kept generating parameter set-ups until 25 locally stable densities when undisturbed. The parameter values of these parameter sets were added together in \( D_i \) to isolate each one of the resource species in each replicate food web of each food web model. This resulted in a total of 365 different parameter set-ups for the single species model. The \( D_i \) of single species counterparts of resource species in FW1M1, FW2M2 and FW3M3 (SS1–SS5) can be found in the electronic supplementary material, table S6. We use this method to keep all parameter values the same as when the species is in its food web. We thereby assume that any differences in species’ environmental response would be the result of adding feedback from species–species interactions.

(c) Environmental variation

Environmental variation influenced single species’ and resource species’ carrying capacity, \( K_i \) (similarly to what is done in previous studies [27,33,41]) via an additive function (as done in [41]):

\[
K_{\text{env}}(t) = K_i (1 + \text{env}(t)),
\]

where \( K_{\text{env}}(t) \) is the carrying capacity affected by environmental variation at time \( t \) (noted more generally as \( K_{\text{env}} \)), \( K_i \) is the mean carrying capacity and \( \text{env}(t) \) is the environmental variation at time \( t \) of resource or single species \( i \). To simplify the comparison between single species and food webs, all resource species were affected by the same environmental variation within replicates. The standard deviation of environmental variation, \( \sigma_{\text{env}} \), was [0.01 0.05 0.1 0.15] for all single and resource species. In the illustrative example with FW1M1, FW2M2 and FW3M3, \( \sigma_{\text{env}} \) was set to 0.15 for the resource species in FW1M1 and FW3M3 and their single species counterparts, and 0.05 for the resource species in FW2M2 and their single species counterparts. \( \sigma_{\text{env}} \) was here normalized based on \( K \) in order to make the effect of environmental variation on resource species’ population dynamics more comparable.

Autocorrelated environmental time series were generated using a 1/f noise-generating method previously used by Lögdberg & Wennnergren [38] (for details see the electronic supplementary material). The environmental noise colour, \( \gamma_{\text{env}} \), will be presented both by units and more generally by the name of the colour. We refer to \( \gamma_{\text{env}} = 0 \) to white, \( 0 < \gamma_{\text{env}} \leq 1 \) to light red, \( 1 < \gamma_{\text{env}} \leq 2 \) to red and \( \gamma_{\text{env}} > 2 \) to dark red noise, in line with earlier studies [38,42]. In the analysis of all food webs, species were exposed to \( \gamma_{\text{env}} = 0 \) and 4. In the mechanistic analysis of FW1M1, FW2M2 and FW3M3, species were exposed to \( \gamma_{\text{env}} \) values between 0 and 4 in steps of 0.2. Both \( \gamma_{\text{env}} = 6 \) and \( \gamma_{\text{env}} = 8 \) were here used as reference values in order to check whether even further increases in positive autocorrelation had any effect on population dynamics (electronic supplementary material, figures S1–S3). We will simplify the notation by referring to the degree of positive autocorrelation in environmental variation as environmental redness.

(d) Data simulation and analyses

From here on, we will refer to the eight different food web models described in figure 1 as ‘the food web models’ or ‘M1–8’,
Table 1. Resource species’ population stability depending on food web model (M1–8), food web interactions, standard deviation (σ_{env}) and colour (white, γ = 0, or red, γ = 4) of environmental variation. The total number of food web parameter set-ups tested was 195 and the total number of resource species was 385. The results are calculated based on food webs without extinctions. Parameter intervals for each model are found in electronic supplementary material, tables S2–S4.

<table>
<thead>
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<th>σ_{env}</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
<th>M4</th>
<th>M5</th>
<th>M6</th>
<th>M7</th>
<th>M8</th>
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<tbody>
<tr>
<td>resource species with higher stability in red than in white environments (%)</td>
<td>0.01</td>
<td>48</td>
<td>41</td>
<td>20</td>
<td>36</td>
<td>32</td>
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<td>14</td>
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<td></td>
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<td>60</td>
<td>11</td>
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<td></td>
<td>0.15</td>
<td>72</td>
<td>28</td>
<td>23</td>
<td>28</td>
<td>23</td>
<td>24</td>
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<td>resource species with higher stability than its single species counterpart in red environments (%)</td>
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<td>52</td>
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<td>35</td>
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<td>49</td>
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<td>64</td>
<td>0</td>
<td>37</td>
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<td>16</td>
</tr>
<tr>
<td>resource species in replicate food webs without extinctions (%)</td>
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</tbody>
</table>

3. Results

(a) Population stability in all food webs

Resource species with higher population stability in red than in white environments were found in all eight food web models (table 1). By contrast, all of the single species counterparts had lower population stability in red than in white environments. The overall percentage of resource species that had higher population stability in a red environment than in a white was 15–28% (28%, 15%, 22% and 24% with σ_{env} = 0.01, 0.05, 0.1 and 0.15, respectively). Replicate food webs with different α_{env} are expected to have different responses to a certain σ_{env}. Thus, we did not expect a simple increase or decrease in the overall percentage of stabilized resource species with increased σ_{env}. While these differences are interesting, they do not affect our main conclusions so we leave a more detailed analysis of these to future work. Independent of σ_{env}, the most common response of replicate food webs was that only one of the resources was stabilized by red environmental variation. There were only one to five replicate food webs (depending on σ_{env}), with at least two resource species, where all resources were stabilized by red environmental variation. When comparing the stability of the resource species and its single species counterpart in a red environment, 35–38% (35%, 38%, 37% and 37% with σ_{env} = 0.01, 0.05, 0.1 and 0.15, respectively) of the resource species were more stable than their single species counterpart.

(b) Mechanistic analysis of food webs with different intrinsic dynamics

Here, we focus on FW1M1, FW2M2 and FW3M3 as they represent different intrinsic population dynamics. One of the resource species in each had higher population stability in...
red environments than in white (figure 2). As presented above, this is the opposite response to what the single species counterpart show. The stabilized resource species, R1FW1M1, R2FW2M2 and R3FW3M3, together with R3FW2M2, also had a minimum stability in light red environments. In order to find explanations for these differing responses to environmental variation, we measured TE of the resource species in FW1M1, FW2M2 and FW3M3. As the response is somewhat complex for food webs with inherent oscillations, we exemplify the connection between population dynamics, environmental variation and TE for FW1M1.

(i) An example of population dynamics
In figure 3, we show the time series of species in FW1M1, the single species counterpart of the resource species in FW1M1 (SS1) and the carrying capacity influenced by environmental variation (Kenv) at three types of environmental conditions. In a white environment (mid-sections of each subfigure in figure 3), the resource species (R1FW1M1) showed high frequent fluctuations, similar to the single species counterpart (SS1). In a red environment, the fluctuations of the resource species differed from its single species counterpart. While the single species followed the environmental variation, the resource species fluctuated as its intrinsic oscillation with minor disturbances of its amplitude (compare the top- and bottom sections of the resource species subfigure in figure 3). Red environmental fluctuations was instead apparent in the dynamics of the second consumer species, C2FW1M1, which fluctuated as a combination of its intrinsic oscillation and the environmental variation (figure 3). Dynamical differences were also found between the stabilized resource species in FW2M2 and FW3M3 and their red environmental variation (electronic supplementary material, figures S4 and S5). But in these two cases, instead of oscillating as R1FW1M1, the resources approached a constant density as their intrinsic state in a constant environment.

(ii) Tracking a fluctuating environment
We measured three types of TE (equation (2.5)) for resource species in FW1M1, FW2M2 and FW3M3, as well as for their single species counterparts. First, we measured the difference between a species' density and carrying capacity (figure 4—TEK). Most of these resource species, together with all of their single species counterparts, improved their tracking of carrying capacity with increased environmental redness. The stabilized resource species also improved their tracking of carrying capacity with environmental redness, but only
in the light red region. Note that R2FW2M2 even tracked its carrying capacity in a white environment better than in a dark red.

Second, we measured the TE between each of the species’ realized density and equilibrium density at each time step (TEE). All resources in FW1M1, FW2M2 and FW3M3, except for R1FW1M1, together with all of the single species counterparts, had lower TEs of equilibrium density in red than in white environments (figure 4—TEE). R1FW1M1 differs in its TEE response because of its intrinsic limit cycles. Resource species with stable limit cycles will have a TE that represents the difference between their equilibrium point and the limit cycles. This difference will appear both in a constant environment and when the species can track its equilibrium in a red environment (figure 3). The difference between R1FW1M1 density and R1FW1M1 equilibrium is larger when the resource has its limit cycles than when the intrinsic dynamics are disturbed and dampened in white environments (for further details see the electronic supplementary material). Note that a similar pattern was found for R2FW2M2 in a light red environment.

Finally, we analysed the TE between equilibrium density and carrying capacity influenced by environmental variation (ETEK). Unlike TEK and TEE, this measure is not affected by the colour of environmental variation (results presented in electronic supplementary material, table S6). The stabilized resource species, R1FW1M1, R2FW2M2 and R3FW3M3, had the largest error between equilibrium density and carrying capacity as well as the largest D values (equation (2.4); electronic supplementary material, table S6). To summarize the results of TE, all resource species in FW1M1, FW2M2 and FW3M3, as well as their single species counterparts, tracked their equilibrium density better in red than in white environments. However, species in food webs might not track their...
carrying capacity influenced by red environmental variation as well as their equilibrium density.

4. Discussion

According to the pioneering studies by May [31] and Roughgarden [32], single species can track their equilibrium densities better in red than in white environments. Thus, single species should have a lower population stability in red than in white environments. However, one could expect that resource species with equilibrium densities strongly repressed by competitors and/or consumers would not track their carrying capacities influenced by red environmental variation equally well as their equilibrium. By studying the species’ population dynamics and their abilities to track equilibrium densities and/or carrying capacities, we here aimed to capture the mechanism behind the potential differences in stability between single species and species embedded in food webs. When we refer to tracking the environmental variation, it is implicit that we refer to tracking the carrying capacity influenced by environmental variation (TEK).

Here, we confirm that the theory of tracking equilibrium densities by May [31] and Roughgarden [32] applies also to food webs. All species in FW1M1, FW2M2, and FW3M3 tracked their equilibrium densities better in red than in white environments (figure 4—TEE). However, the degree of redness differed between species and type of food web. Furthermore, to understand how species in food webs with intrinsic limit cycles fit into this conclusion of tracking equilibria, it is important to remember that their densities oscillate when unperturbed. The oscillations around constant equilibrium points result in high TE of equilibria (TEE), even in a constant environment. Thus, in the case of FW1M1 in red environments, we expected a TEE of a similar value as when unperturbed (figure 3; see the electronic supplementary material, figure S6 for more details on the subject).

Varying the carrying capacity of resource species is a continuous enrichment/depletion of a system. It is therefore relevant to consider the theory of paradox of enrichment [43] together with top–down and bottom–up control in food webs [4,44–46] when interpreting the results of different food webs exposed to red environmental variation. The paradox of enrichment stems from the study of a predator and its prey and how their equilibrium densities depend on prey carrying capacity: an increase in prey carrying capacity leads to an increase in the equilibrium density of the predator instead of in the equilibrium density of the prey. A similar result can be found in longer food chains, where adding a trophic level may result in a trophic level shift of the enrichment response [45,47]. Recently, Wollrab et al. [46] showed that similar results also can be found for branched food chains. Our findings that some species in more complex food webs were able to track the fluctuating environment.

Figure 4. Population TE of fluctuating carrying capacity (TEK) and equilibrium density (TEE). Row (a) shows results of the resource species in FW1M1 and its single species counterpart, (b) the resources in FW2M2 together with the single species counterparts and (c) the resources in FW3M3 together with their single species counterparts. Stabilized resource species (R1FW1M1, R2FW2M2, R3FW3M3) have TEs that differ from those of their single species counterparts (SS1, SS2 and SS3).
carrying capacity while others were not expand the paradox into fluctuating environments: the stabilized resource species, which did not track the fluctuating carrying capacity in red environments, resembles the prey in the predator–prey paradox theory in which equilibrium was unaffected by enrichment.

The stabilized resource species had large TEs between equilibrium densities and carrying capacities (ETEK), as well as large totals in species–species interaction coefficients at equilibrium, D (electronic supplementary material, table S6). This infers a strong dampening from species–species interactions. The environmental variation was in these cases transferred from the resource species to another species with less dampening from species–species interactions (figure 3 and electronic supplementary material, figures S4 and S5). Thus, the extent of food web feedback on equilibrium densities completely determines population dynamics in red environments (figure 2). When considering all food web models, models seven and eight are closely related to a simple food chain with three trophic levels [45,47]. We expect to find that these have an enrichment effect on resource and predator trophic levels when the species are able to track changes in their equilibrium. The resource species in food web model seven will be perceived by the consumer as one because of the synchronized environmental variation. This explains why there were so few stabilized resource species in food web models seven and eight (table 1).

In dark red environments, the results are well explained by the theories of May [31] and Roughgarden [32] and the paradox of enrichment [43]. However, when comparing results between white and red environments, the response can be more complex (for an extended discussion regarding resource species in FW1M1 and FW2M2, see the electronic supplementary material). The TE of the environmental variation (TEK) decreased for all resource species in FW1M1, FW2M2 and FW3M3 in the initial range of redness (figure 4). In the latter range, TEK instead increased for the stabilized resource species as they could start to track their equilibrium density. We suggest that the minimum in stability (figure 2) and maximum in variance (electronic supplementary material, figures S1–S3) observed for the stabilized resource species in light red environments (and to some extent also for Rs3W2M2) can be explained by transient population dynamics. The amplitudes of the species' transient dynamics would increase between white and light red noise as the TE of environmental variation decreases. Between light red and red noise, the species starts to track its equilibrium better than its environmental variation. This would result in a decrease in transient amplitudes until the transients completely disappear when the species tracks its equilibrium in dark red noise.

Another possible explanation of the minimum in population stability could be a resonance effect [30,48]. Such a mechanism implies a population variance peak when the frequencies of environmental variation and population dynamics coincide. Based on our analysis, we did not interpret the minimum in stability as a resonance effect. Instead of a resonance peak, our results show a slow increase followed by a slow decrease or no change in population variance with increased environmental redness (electronic supplementary material, figures S1–S3). To summarize our analysis of the stabilized resource species, the minimum in stability in light red environments emerged as a result of a duel between environmental variation causing transient dynamics and the stabilizing forces of intrinsic dynamics pushing the population towards a stable equilibrium [4,9]. The continuous increase in stability towards a maximum value, between red and dark red environmental variation, was the sole result of an increase in the stabilized resource species' abilities to track their constant equilibria.

5. Conclusion

Species–species interactions do not change species' response to white (uncorrelated) environmental variation nor their abilities to follow equilibrium densities affected by environmental variation. However, adding species–species interactions to a single species when affected by red (positively autocorrelated) environmental variation can result in a complete change in population dynamics, and thereby also their stabilities. For natural ecosystems, this indicates that shifts in environmental variability, caused for example by climate change, can cause large and unexpected changes in the dynamics of populations. Our results suggest that food web effects, such as top–down/bottom–up control and cascading extinctions, will have larger consequences with increased redness in the environmental variation. In order to make good predictions of how species respond to changes in environmental variability, it is necessary to consider species' interaction together with environmental autocorrelation. Natural variation is mostly considered to be positively autocorrelated. By disregarding this complexity, conservation efforts may very well miss their targets.

Authors' contributions. S.G. carried out the modelling and data simulation work, participated in the design of the study, participated in data analysis and drafted the manuscript; A.E. participated in the design of the study, participated in data analysis and helped draft the manuscript; U.W. coordinated the study, participated in data analysis and helped draft the manuscript. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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