The predictability of ecological stability in a noisy world

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Random environmental variation, or stochasticity, is a key determinant of ecological dynamics. While we have some appreciation of how environmental stochasticity can moderate the variability and persistence of communities, we know little about its implications for the nature and predictability of ecological responses to large perturbations. Here, we show that shifts in the temporal autocorrelation (colour) of environmental noise provoke trade-offs in ecological stability across a wide range of different food-web structures by stabilizing dynamics in some dimensions, while simultaneously destabilizing them in others. Specifically, increasingly positive autocorrelation (reddening) of environmental noise increases resilience by hastening the recovery of food webs following a large perturbation, but reduces their resistance to perturbation and increases their temporal variability (reduces biomass stability). In contrast, all stability dimensions become less predictable, showing increased variability around the mean response, as environmental noise reddens. Moreover, we found environmental reddening to be a considerably more important determinant of stability than intrinsic food-web characteristics. These findings reveal the fundamental and dominant role played by environmental stochasticity in determining the dynamics and stability of ecosystems, and extend our understanding of how the multiple dimensions of stability relate to each other beyond simple white noise environments.

Predicting how ecosystems will respond to global environmental change has become a central focus of ecological research[1–7]. The prediction of ecological responses typically involves the use of static approaches that focus on mean levels of environmental change, such as warming and deforestation[8,9]. Many approaches overlook environmental stochasticity, which introduces uncertainties and, even when incorporated, is usually considered a purely random term. However, stochasticity has structure and comprises a key determinant of the dynamics and structure of populations and communities[10,11]. Exploration of its underlying characteristics, such as its variance and temporal or spectral structure[12–14], reveals, for example, the frequency and duration of extreme events, and determines the variability and persistence of populations[8,15–21]. For example, Ruokolainen et al.[13] reviewed how predictable outcomes for population variation depend on the interplay between population density dependence (that is, under-, over- or purely compensatory dynamics) and the structure of the autocorrelation in environmental stochasticity. Briefly, red noise (positive autocorrelation) is expected to be amplified at the population level in (deterministically) slow-growing (undercompensatory) populations, but dampened in rapidly growing (overcompensatory) populations, and vice versa for blue noise (negative autocorrelation). However, despite its overarching influence on population and community dynamics, the role played by environmental stochasticity in moderating ecological responses to other perturbations—particularly large perturbations—remains mostly unknown.

Ecological stability is a multidimensional concept that tries to capture the different aspects of the dynamics of the system and its response to perturbations[9,22,23]. The concept is fundamental to the conservation and management of natural resources[9] and has been a central focus of ecological research for decades[23–25]. The various dimensions of stability, such as the variability of community biomass in time and space, and the resistance and resilience of communities (that is, their capacity to, respectively, resist and recover from perturbations) have, however, typically been considered in isolation, due in part to the difficulty of quantifying them simultaneously in the natural world[9]. Moreover, their behaviour and predictability probably depend strongly on the spatiotemporal range across which they are estimated[26]. Stability components such as variability and persistence (that is, the length of time a system maintains the same state before it changes in some defined way[23]) are usually estimated from long-term dynamics and are therefore more likely to reflect key features of environmental stochasticity. In contrast, stability components that describe the responses of communities to distinct perturbations, such as resistance and resilience, are determined within shorter time windows. They are consequently likely to be sensitive to the timing and duration of potential extreme events. This makes them less predictable (that is, they show greater variation around the mean community response). Nonetheless, their general response pattern can still be revealed by examining and averaging the stability of many similar systems experiencing the same environmental perturbations.

Here, we explore how three key components of ecological stability (Fig. 1)—recovery time (the reciprocal of resilience); the extent of change in community structure in response to perturbation (a measure of resistance; a larger extent of change indicates weak resistance[22,23]); and variability—are regulated by environmental stochasticity. We use simulated model food-webs described by the general Lotka–Volterra system[27–29] to examine both the responses and predictability of these stability components along gradients of the key factors that characterize environmental stochasticity—its temporal autocorrelation (that is, its colour[14,20]) and the correlations in species responses to it[13,14,20,21,30]. As predators tend to be particularly important drivers of community dynamics and, consequently, predator loss is considered to be one of the most profound biotic perturbations that can occur[7,31–33], we perturbed our model systems by reducing the densities of the apex predator in each food web by

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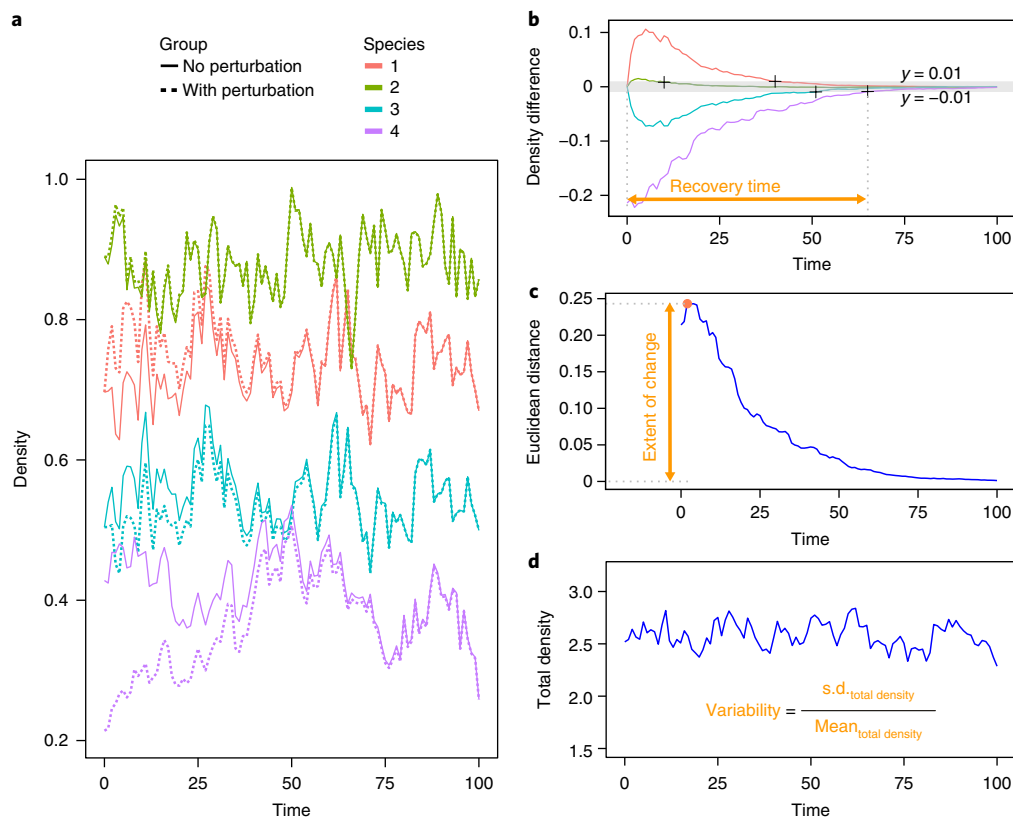
Fig. 1 | Quantification of ecological stability dimensions. a, A typical example of community dynamics. **b**, Species density difference between perturbed and equivalent unperturbed communities at each simulation time step. The recovery time was quantified as the moment when the species density difference was smaller than 0.01 for all species (indicated for each species by a plus sign; see Methods). **c**, Extent of change of the community (our measure of resistance), quantified as the largest Euclidean distance between perturbed and equivalent unperturbed communities. **d**, Variability was quantified as the s.d. of the total density of the unperturbed community divided by its mean value.

50%, as a single pulse perturbation, coupled with short-term, continuously fluctuating coloured environmental variation.

Given the significant disjoint between many theoretical measures of stability and what can be measured empirically[9], we quantified all components of stability empirically across a broad range of four-species food-web modules (Supplementary Fig. 1; including, for example, simple food chains, modules including omnivory and/or apparent competition)—subnetworks of tightly interacting species that act as the 'building blocks' of food webs[34–36] —to explore the generality of our findings. Our results revealed highly consistent patterns across all types of food webs explored, and demonstrate contrasting patterns across different stability dimensions and increasing uncertainty in community responses under redder environments.

Results

To illustrate our findings, we focus initially on the effect of temporal autocorrelation on the dynamics of one randomly assembled community, from what is the simplest food-web module—the food chain (that is, module 1 in Supplementary Fig. 1). We then expand our focus to 100 replicate communities from each of 14 food-web modules to explore the generality of our results (Supplementary Fig. 1).

Increased temporal autocorrelation (reddening) of environmental stochasticity both stabilized and destabilized the example food-chain community along different dimensions of stability (Fig. 2a). Increasing autocorrelation from negative (blue) to positive (red) destabilized the community by increasing both total biomass variability and the extent of change in community structure (that

is, reducing resistance) in response to the initial, large perturbation. Simultaneously, environmental reddening enhanced stability by reducing the recovery time after the perturbation (that is, increasing resilience; Fig. 2a). In contrast, the uncertainty (coefficient of variation) in all stability responses increased consistently with environmental reddening (Fig. 2b), indicating that higher temporal autocorrelation reduces the predictability of ecological stability, at the scale of individual food-web responses.

Results from the example food-chain community were consistent not only with those from the other communities with the same module structure, but also with those from across all other modules examined (Fig. 3). Recovery time decreased with environmental reddening, while the extent of community change and biomass variability both increased (Fig. 3a). Furthermore, the predictability of all dimensions of stability decreased monotonically as environmental autocorrelation increased, as the uncertainty (coefficient of variation) across individual food-web responses more than doubled in every case as the noise colour changed from blue to red (Fig. 3b).

The correlation in species responses to environmental fluctuations modified the specific response of both recovery time and variability, but had little effect on the extent of community change (Fig. 4a). When correlations in species responses to environmental fluctuations were weak, communities showed lower biomass variability (that is, increased stability) compared with when they were strong. However, weaker correlations in species environmental responses simultaneously destabilized communities by increasing the recovery time compared with when they were strong (Fig. 4a). There was no
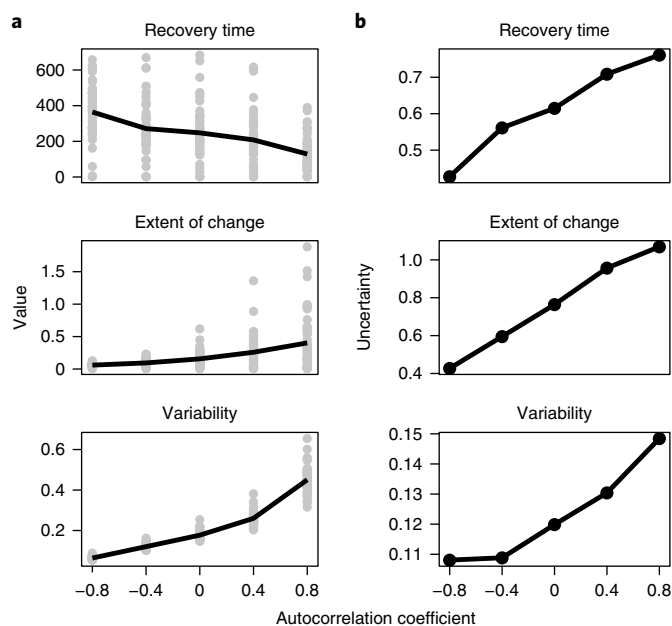
Fig. 2 | Stability responses of a single food-chain community to replicate regimes of environmental stochasticity along a gradient in temporal autocorrelation. a, Changes in recovery time, the extent of change in community structure and variability in a single example food-chain community along a gradient in temporal autocorrelation. Every point at each level of autocorrelation represents the stability response of 1 of 50 noise replicates (distinct runs of stochastic noise described by identical autocorrelation; see Methods) for the community. All responses are inversely related to stability (that is, stability decreases from the bottom to the top of the y axis in every case). The solid line corresponds to the mean response for the community across noise replicates and therefore indicates the general response of each stability component to the temporal autocorrelation of environmental noise. **b**, Uncertainty in stability responses of the community to the temporal autocorrelation of environmental noise. This was quantified as the coefficient of variation (s.d. divided by mean) across the noise replicates. High uncertainty corresponds to low predictability of ecological stability. For this illustrative example, the correlation of species responses to environmental fluctuations was set to 0.2.

general effect of correlations in species–environment responses on the uncertainty of any of the stability components (Fig. 4b).

Variation in the general response of all stability components analysed was almost entirely accounted for by the explanatory variables included in our random forest regression models (pseudo-R^2 values ≥ 0.98 in every case; Fig. 5a). However, the models accounted for significantly lower variation in the specific responses of stability components to distinct runs of stochastic noise (the regression pseudo-R^2 of recovery time, extent of community change and variability were reduced to, respectively, 0.38, 0.35 and 0.72; Fig. 5a). These reductions in explanatory power were particularly acute for resistance and resilience, consistent with the high uncertainty associated with these stability components in previous analyses (Fig. 2b and Fig. 3b).

The temporal autocorrelation of environmental stochasticity was the dominant determinant of both the general and specific responses of all stability components examined (Fig. 5b). Species environmental response correlations had a far weaker effect on stability dimensions than temporal autocorrelation, and contributed little to the general response of any stability component, although they had some influence on the specific temporal response of communities in terms of their recovery time and variability (Fig. 5b). Compared with these components of environmental stochasticity,

both community and module characteristics were of minor importance in determining stability (Fig. 5b).

Discussion

Although environmental stochasticity plays a critical role in determining the assembly, diversity, evolution and functioning of ecological communities[13,30,37,38], it is commonly treated as synonymous with fundamental unpredictability. In contrast, our results demonstrate that key aspects of environmental stochasticity can regulate ecological stability responses in a predictable way. Within the given range of the parameters of our models, we identified the two key factors that characterize stochasticity—its temporal autocorrelation and the correlations in species responses to it—as more important determinants of ecological stability than any inherent characteristics of community or module structure. Moreover, we found that the effects of environmental stochasticity on the responses and uncertainties associated with different components of ecological stability are highly consistent across a large variety of food-web structures. These findings highlight the fundamental importance of applying environmental stochasticity to illuminate our understanding of—and enhance significantly our capacity to predict—the different dimensions of ecological stability in communities.

Shifts in both the temporal autocorrelation of environmental noise and correlations of species responses to it provoked trade-offs among components of stability by stabilizing communities in some ways but simultaneously destabilizing them in others. The reddening of environmental noise reduced the recovery time (that is, increasing resilience) while simultaneously increasing both the extent of change in response to perturbation (that is, reducing resistance) and variability. Moreover, these effects were amplified when correlations in species responses to environmental fluctuations were strong. In general, as was the case in our study, increasing environmental reddening amplifies the fluctuations in population density in undercompensatory populations[13,39,40]. Increases in both variability and the extent of change in response to perturbation were a consequence of the propagation of this enlarged population (and community) variance as environmental stochasticity reddened. Furthermore, the higher temporal variability of both populations and communities in red noise environments more rapidly overwhelmed the effect of the initial perturbation, bringing the perturbed and unperturbed communities into more similar stochastic biomass envelopes (shaded bands in Fig. 1b) with the same environmental stochasticity, consequently reducing the recovery time. Increasing correlations of species responses to environmental noise enhanced this effect further by increasing species synchrony, which reduced the buffering effect caused by species responding in more diverse ways to environmental fluctuations[41–44].

Our findings highlight the challenges in predicting ecological stability on local temporal and spatial scales. Despite the trade-off that occurred among components of stability as temporal autocorrelation changed, their uncertainty increased consistently as environmental noise reddened. When environmental colour changes from blue through white to red, populations experience longer runs of extreme conditions[40]. As undercompensatory populations are slow to track environmental change, longer runs of extreme conditions are then translated into longer runs of low (or high) total biomass densities. The increase in the duration of extreme runs increases the variability of recovery time as long runs of good environmental conditions reduce the recovery time by helping the community recover quickly from the initial large perturbation, while long runs of poor environmental conditions increase the recovery time by making it harder for the community to return to the equilibrium envelope. Likewise, long runs of poor environmental conditions will tend to amplify the initial large perturbation more than long runs of good conditions (which will tend to cancel it out quickly, bringing the community back to the equilibrium envelope).
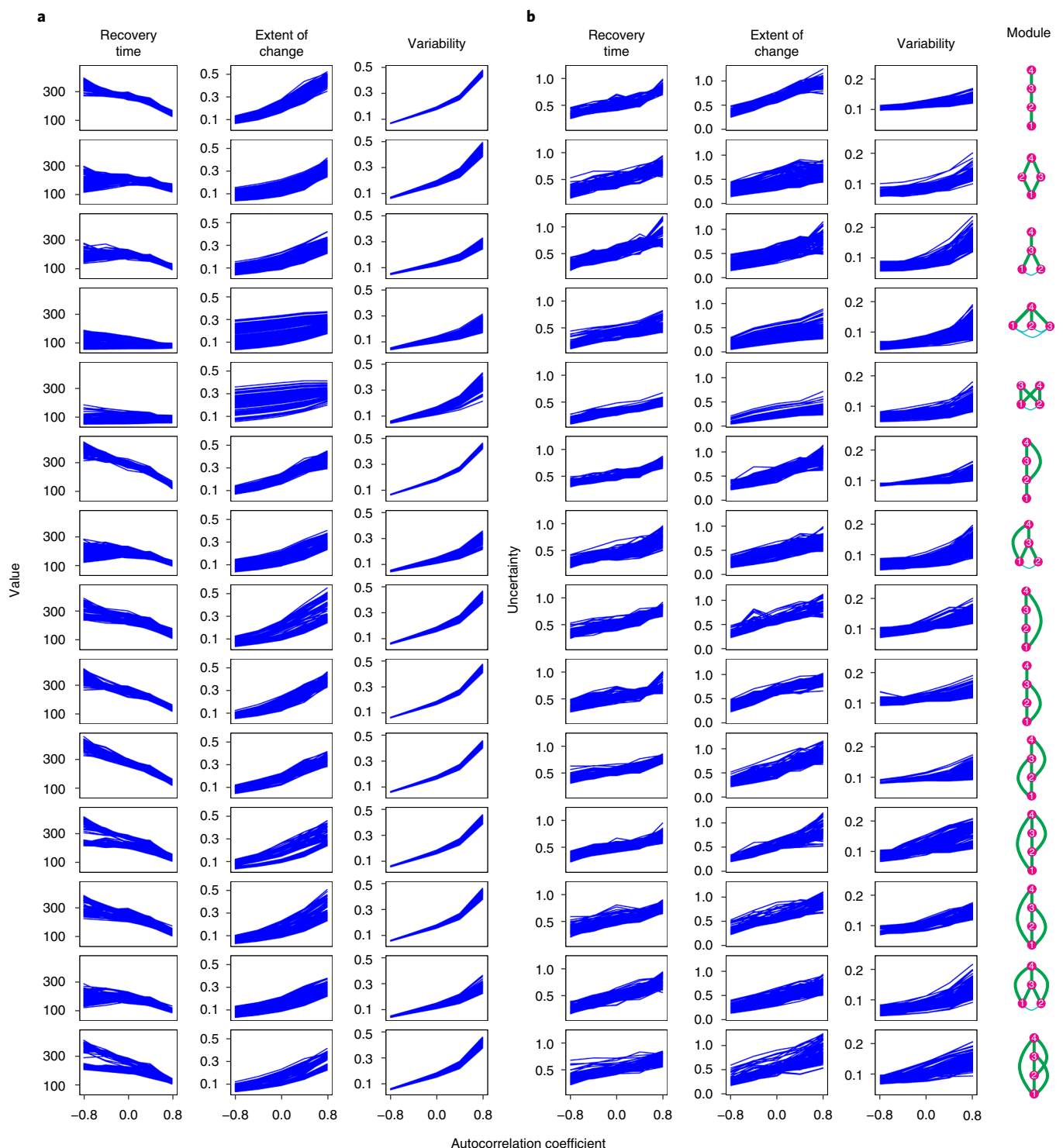
Fig. 3 | General stability responses to changes in environmental autocorrelation across a diverse range of food-web modules. a,b, General stability responses (**a**) and uncertainty of those responses (**b**) to changes in environmental autocorrelation. Individual lines in **a** and **b** correspond, respectively, to the mean and coefficient of variation in the response across 50 noise replicates for each of the 100 communities of each module structure. All responses in **a** are inversely related to stability (that is, stability decreases from the bottom to the top of the *y* axis in every case). For this illustrative example, the correlation of species responses to environmental fluctuations was set to 0.2.

This means that, under a run of poor conditions, the extent of community change will be larger under red than blue/white noise as the poor conditions drag the initial perturbation further from the equilibrium envelope, while under a long run of good conditions, the community is taken less far from the equilibrium envelope than under blue/white noise. All of these together resulted in higher uncertainty, and thus lower predictability, in the extent of community change under red than blue/white noise.

Our results also show that recovery time and resistance are much more difficult to predict than biomass variability. This is probably a
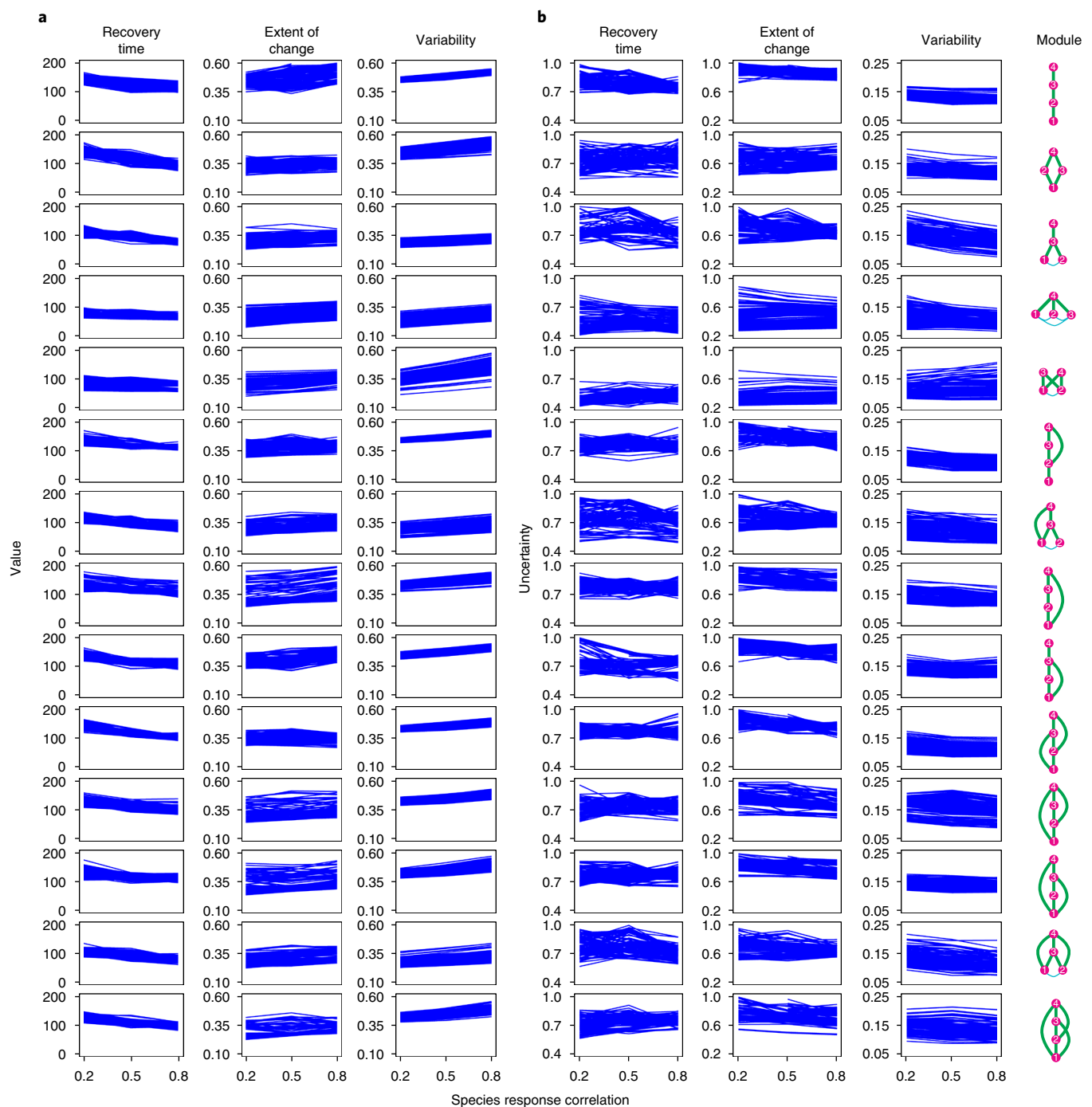
Fig. 4 | General stability responses to changes in the correlation of species responses to environmental fluctuations across a diverse range of food-web modules. a,b, General stability responses (**a**) and uncertainty of those responses (**b**) to changes in species environmental response correlations. Individual lines in **a** and **b** correspond, respectively, to the mean and coefficient of variation in the response across 50 noise replicates for each of the 100 communities of each module structure. All responses in **a** are inversely related to stability (that is, stability decreases from the bottom to the top of the y axis in every case). For this illustrative example, the temporal autocorrelation of environmental noise was set to 0.8.

consequence of the difference in time ranges across which these different dimensions of stability are quantified. Resistance and recovery time were quantified from discrete time points within a relatively short time window. Over increasingly short time ranges, the relative importance of distinct patterns in the timing and duration of a few individual extreme events across the ($n = 50$) different replicate runs of environmental stochasticity is enhanced, reducing the ratio of signal to noise, and leading to a large variance in resistance and recovery time among replicates. In contrast, biomass variability was

measured across the whole simulation time, which is likely to reflect stochastic structure much more closely as the effects of multiple individual extreme events are averaged out. Consistent with this, shortening the time window over which variability was quantified increased its uncertainty significantly (Supplementary Fig. 2). This mechanism is also likely to be responsible for the lack of importance of species environmental response correlations in determining the extent of community change in response to perturbation. Over the relatively short time periods during which the extent of community
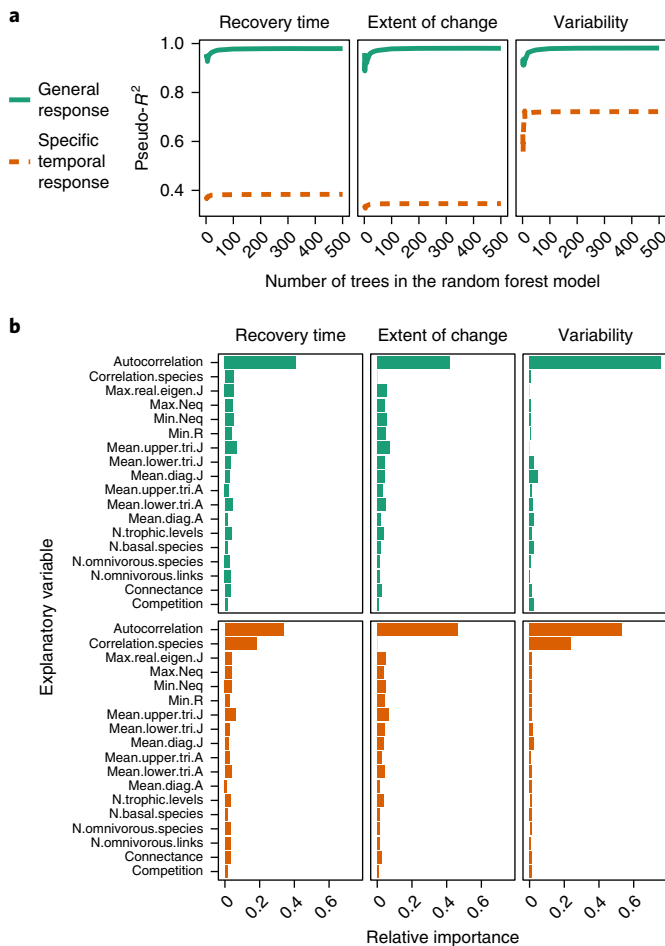
Fig. 5 | Determinants of ecological stability in stochastic environments.
a, Explanatory power (pseudo-R^2 of random forest regression models) of
environmental stochasticity and community and module characteristics
in determining both the general response pattern (the mean stability
response across noise replicates; $n = 21,000$) and the specific temporal
response (that is, incorporating variation in the responses of food webs
to distinct runs of stochastic noise described by identical autocorrelation;
$n = 1,050,000$) of stability components to environmental autocorrelation.
b, Relative importance of individual determinants of stability (top, general
response (green); bottom, specific temporal response (orange)), calculated
as the importance value of each explanatory variable in random forest
regression models divided by the sum of the importance of all variables.
The following variables were included as determinants in the model: the
autocorrelation coefficient of environmental stochasticity (autocorrelation);
the correlation of species responses to environmental noise (correlation.
species); the maximum real part of the eigenvalue of the community
matrix (max.real.eigen.J); the maximum equilibrium species density (max.
Neq); the minimum equilibrium species density (min.Neq); the slowest
growth/decay rate of the community (min.R); the mean value of the
upper triangular (mean.upper.tri.J), lower triangular (mean.lower.tri.J) and
diagonal (mean.diag.J) entries of the community matrix; the mean value of
the upper triangular (mean.upper.tri.A), lower triangular (mean.lower.tri.A)
and diagonal (mean.diag.A) entries of the interaction coefficient matrix;
the number of trophic levels (n.trophic.levels), basal species (n.basal.
species), omnivorous species (n.omnivorous.species) and omnivorous
links (n.omnivorous.links); food-web connectance (connectance); and the
presence of competitive links between basal species (competition).

change was measured, the impact of the single, large perturbation
overwhelmed any effect that correlations of species environmental
responses could exert on this stability dimension.

The complex and hierarchical nature of ecology provides a key
challenge for predicting ecological stability in stochastic environ-
ments. For simplicity, we used four-species food-web modules as the
basic structure of the biological community. Although these include
some of the most common building blocks of the ecological networks
found in nature[34–36] and have been used broadly to study ecological
stability and both environmental and demographic stochasticity,
they nonetheless omit some important biological details that could
affect how biological communities respond to environmental sto-
chasticity. For example, demographic stochasticity and variation in
realized vital rates through age, stage, genetic, behavioural, spatial
or other biological structure can all modify population responses
to environmental variation[11]. These factors may either be affected
directly by environmental stochasticity or may regulate the impact of
environmental stochasticity on other biological or ecological charac-
teristics. For example, our models assume the interaction coefficient
a_{ij} (see Methods) to be constant (that is, consumption by consumers
increases linearly across all prey densities, similar to Holling's type
I functional response). In nature, depending on the body size ratio
between the consumer and the resource species, consumers may
follow type I, II or III functional response patterns[45]. Although the
choice of functional response curve could influence system dynam-
ics, we would nonetheless expect qualitatively similar shifts in the
stability characteristics of the system with changes in the temporal
autocorrelation of environmental noise (Supplementary Table 1; see
also Kaneryd et al.[46]). While including all of the biological complexi-
ties we describe above together with environmental stochasticity
would result in a highly complex model, incorporating a subset of
the biological details in the proper candidate stochastic model may
reveal the interplay between key biological details and environmen-
tal stochasticity in determining ecological stability. For example, the
allometric trophic network model[47] may reveal how environmental
stochasticity affects ecological stability through regulation of meta-
bolic rates, either through direct regulation of the metabolic rate or
indirect regulation via changing the body mass/size of individuals.

In our study, all three stability measures are based on the
assumption of the existence of a unique stable-point equilibrium
in the food webs, and our community assembly process ensured
that this was the case. However, ecosystems can shift from one sta-
ble state to another type of equilibrium as a consequence of either
strong environmental forcing or positive feedback from the sys-
tem[24,48]. Environmental stochasticity may prevent the community
from arriving at its deterministic equilibrium in at least three ways.
First, for a deterministic system prone to bifurcation or chaos, the
existence of environmental stochasticity will inevitably increase the
unpredictability of the system's dynamics in some way. Second, as
slow trackers of environmental change, undercompensatory popu-
lations may present strong positive autocorrelation in their dynam-
ics under red noise and may therefore be more prone to regime
shifts[49]. Third, sufficiently large environmental stochasticity can
cause the community to fluctuate around its equilibrium—either
a stable point or a limit cycle—within a characteristic distribution.
In systems close to a bifurcation boundary, stochasticity can cause
the system to appear to switch to a qualitatively different type of
dynamical behaviour, such as from fluctuating around a stable-
point equilibrium to fluctuating around a cycle[50]. The determinis-
tic negative feedback inherent in consumer–resource interactions
can, for example, make these systems prone to cycling[51]. When the
cycles are transient (that is, damped oscillations), systems will settle
onto a point equilibrium in the absence of stochasticity. However,
with stochasticity, the same systems may exhibit sustained cycles[50].
In this way, stochasticity can provoke qualitatively different dynam-
ics in ecosystems that would not otherwise be apparent.

For simplicity and tractability, we controlled the variance of
environmental stochasticity at the same level, and assigned set
levels of species response correlations to environmental fluctuations

for all consumers and basal species, whose populations all exhibit undercompensatory dynamics. In nature, communities consist of both overcompensatory and undercompensatory populations, each of which could respond in different ways to environmental stochasticity. Moreover, different species experience different levels of stochasticity across multiple environmental factors all the time. These complexities may scale up to affect ecosystem stability by propagation through the linear, nonlinear and higher-order interactions[52] between the other components of the system. Predicting the outcomes of these processes is a complex challenge. However, our findings demonstrate that incorporating key characteristics of environmental stochasticity into our models is an essential step towards improving prediction in ecological systems. Moreover, understanding how different elements of human-induced global environmental change modify the temporal and spatial autocorrelation of environmental noise is necessary to provide improved understanding and prediction of ecosystem stability.

Methods

Food-web construction and simulations. We constructed sets of 14 distinct four-species food-web modules (Supplementary Fig. 1) to cover a large range of different network structures that vary in both trophic topology and connectance. We then constructed 100 individual communities within each set of module structures. The dynamics of our modules are described by the general Lotka–Volterra system[27–29]:

$$\frac{dN_i(t)}{dt} = N_i(t)\left(r_i + \sum_{j=1}^{4} a_{ij}N_j(t) + \varepsilon_i(t) \right) \tag{1}$$

where i and j are the identities of species in the community, N_i is the population density of species i, r_i is the intrinsic growth/mortality rate (positive for basal species; otherwise negative), a_{ij} is the interaction coefficient that describes the per-capita effect of the jth species on the growth/mortality rate of the ith species (positive if it enhances population growth; negative if it causes decreases in growth) and $\varepsilon_i(t)$ is the species-specific response to environmental stochasticity (see below).

We followed Petchey et al.[29] to parameterize the models. We first set the growth rates of basal species to 1, and drew mortality rates (that is, the intrinsic rate of change in the absence of resources and predation) of consumers randomly from a uniform distribution. Petchey et al.[29] drew mortality rates from −0.001 to 0. As our food-web modules have fewer species but more trophic levels, we drew mortality rates from −0.001 to −0.1 instead to avoid extremely small mortality rates of consumers, particularly the top consumer. We sorted the mortality rate so that predators had lower mortality rates than their prey, as species at higher trophic levels tend to be larger[53] and large size generally leads to greater longevity and low mortality rates[54,55]. The value of the per-capita effect of the consumer on its resources a_{ij} was assigned depending on the number of resource species. When the consumer fed on only one species, a_{ij} was set to 0.5. Otherwise, a randomly chosen link was given one strong interaction coefficient (set to 0.4), and other links were assigned weak interactions and set to 0.1 divided by the number of resources minus 1. This approach resulted in a skewed distribution of interaction strengths, which is commonly found in real ecological networks[56,57]. The per-capita effect of the resource species on its consumer a_{ji} was calculated as a_{ij} multiplied by the conversion efficiency. We set the conversion efficiency of non-omnivorous links to 0.2 and that of omnivorous links to 0.02 by assuming that it takes more mass of the basal species (plants in most situations) than animals to produce one predator offspring[29]. Intraspecific competition occurred in all species and was set to 1 for basal species and 0.1 for other species. Interspecific competition among basal species was modelled by setting the appropriate competition coefficients (drawn randomly from the uniform distribution 0 to 0.5). Interspecific competition among consumer species was indirect through the consumption of shared resources[29].

Using the interaction coefficient matrix A, with entries a_{ij}, and the vector $\mathbf{R}$, with entries of r_i, we estimated the density of species at equilibrium, N_i^*. At equilibrium, the per-capita change rate of all species is zero, so $A\mathbf{N}^* = -\mathbf{R}$. Then, $\mathbf{N}^*$ can be solved as $\mathbf{N}^* = -A^{-1}\mathbf{R}$, where A^{-1} is the inverse of matrix A. The equilibrium Jacobian interaction matrix J^* (also known as the community matrix), with entries J_{ij}, which is used to test the local stability of the constructed community[25], is derived by $J_{ij} = a_{ij}N_i^*$. When the maximum real part of the dominant eigenvalue of the community matrix is negative, the deterministic system will settle to a stable-point equilibrium. However, if this negative eigenvalue is close to zero, the system approaches a bifurcation threshold. To ensure against alternative full coexisting stable states (for example, limit cycles or chaotic fluctuations) by stochastic resonance, we excluded communities whose maximum real part of the dominant eigenvalues was larger than −0.005 (see Supplementary Fig. 3 for the realized distributions of the maximum real part of the eigenvalues from our model communities). This is sufficiently far from the bifurcation threshold to avoid the system shifting to another dynamical attractor under the

stochastic variation we considered. The process of parameterization continued until, for each of the 14 food-web modules, we constructed 100 communities that satisfied the requirements of both local stability and feasibility[58–60]. The equilibrium species densities of communities generated by this method conformed to the pyramidal structure, with species of lower trophic levels being more abundant (Supplementary Fig. 4).

Environmental stochasticity. The effect of environmental stochasticity was incorporated in the dynamical system of equation (1) by the continuous variable $\varepsilon_i(t)$, which represents the specific response to environmental stochasticity. When the time step is small, $\varepsilon_i(t)$ can be approximately represented by the discrete variable $\varepsilon_i(T)$, which is given by the autoregressive process[30] as:

$$\varepsilon_i(T+1) = k\varepsilon_i(T) + \sigma\sqrt{1-k^2}\ \frac{\varphi(T) + \beta\omega_i(T)}{\sqrt{1-\beta^2}}$$

$$\beta = \sqrt{\frac{1-|\rho|}{|\rho|}} \tag{2}$$

where T is the discrete time point (0, 1, 2… 1,000), k is the autocorrelation coefficient and ρ is the species response correlation (that is, the correlation between all pairs of specific response ε_i). The terms $\varphi(T)$ and $\omega_i(T)$ are standard normal random components, where $\varphi(T)$ is consistent for all species and $\omega_i(T)$ differs between species. Parameter β is a scaling factor ensuring that noise variance remains independent of ρ. This method scales the noise time series to its asymptotical variance σ_i^2 independent of noise autocorrelation[30,61]. We simulated a range of regimes of environmental stochasticity within a fully crossed design using k and ρ. k was set to −0.8, −0.4, 0, 0.4 and 0.8, reflecting ranges in colour from blue through white to red, while ρ was set to 0.2, 0.5 and 0.8 (with 0 corresponding to no correlation among species and 1 corresponding to perfect correlation). Therefore, there were 15 (that is, 5 × 3) fully crossed combinations of k and ρ. We arbitrarily set σ_i^2 to 0.05 for simplicity. Changing the level of σ_i^2 does not affect our conclusions about the general effects of environmental stochasticity on the response or predictability of ecological stability (Supplementary Fig. 5). The unique combination of stochasticity features all led to different stochasticity regimes determined by the random terms $\varphi(T)$ and $\omega_i(T)$. We produced 50 sets of $\varphi(T)$ and $\omega_i(T)$, and applied them to each unique combination of stochasticity features to build 50 'replicated' regimes of environmental stochasticity, which were then used for every model community.

Most models comparing coloured environments with white noise assume implicitly that the normality of the noise time series is retained as its temporal autocorrelation changes from zero to either positive or negative values[40,62]. However, Fowler and Ruokolainen[63] showed that coloured series tend to deviate from the normal distribution when using common approaches to generate time series of coloured environmental stochasticity, and this can confound the effect of environmental colour on dynamical processes. Cohen et al.[64] developed the 'spectral mimicry' approach to transform a coloured environmental series that does not follow a normal frequency distribution to a new series with a normal distribution yet maintaining the original level of temporal autocorrelation. Briefly, spectral mimicry takes two input series of equal length, $\mathbf{X}$ and $\mathbf{Y}$, and reorders one series ($\mathbf{Y}$) to generate a third series ($\mathbf{Z}$) that approximates the temporal characteristics (colour) of $\mathbf{X}$. $\mathbf{X}$ is a traditional-coloured series that was generated by the autoregressive process defined by equations (1) and (2), and $\mathbf{Y}$ is an independent random series drawn from a normal distribution (mean = 0; variance = 0.05). Only random series $\mathbf{Y}$ that failed to reject the null hypothesis of a Jarque–Bera statistical test (that is, that there is no evidence that data deviate from a normal distribution; significance level $a = 0.05$) were selected for further use. The elements of $\mathbf{X}$ were ranked in increasing value, with their order statistics recorded from the original series. Series $\mathbf{Z}$ was then generated from $\mathbf{Y}$ "by replacing each element of $\mathbf{Y}$ by the corresponding order statistic of $\mathbf{X}$"[64]. This algorithm results in series $\mathbf{Z}$ having a spectral exponent similar to that of $\mathbf{X}$. For each environmental stochasticity time series generated using the autoregressive process (equation (2)), we used spectral mimicry to generate another time series to avoid artefacts in the results known to be caused by traditional AR(1) methods[63]. Both the autoregressive method and spectral mimicry produced the desired temporal autocorrelation and species response correlation (Supplementary Figs. 6 and 7). For simplicity, we report only the results that used spectral mimicry to generate environmental stochasticity, although the general features of our results are consistent with those from autoregression. In summary, we produced $5(k) \times 3(\rho) \times 50(\text{realizations}) = 750$ stochasticity regimes for each of our 1,400 communities (100 communities × 14 modules).

Ecological stability. We simulated species dynamics for all food webs with the locally stable equilibrium as the initial state value for every replicate stochasticity regime. In parallel, we also simulated their dynamics with a 50% reduction in the equilibrium biomass of the species at the highest trophic level in each food-web module as the initial state value under the same stochasticity regime. This corresponded to the 'perturbed' treatment for each replicate stochasticity regime. Coupling the simulations with and without initial perturbation adds ecological

realism compared with previous studies, which tend to investigate only one of them (but see ref. [65]). Simulations of dynamics of both the 'unperturbed' and 'perturbed' community were run over 1,000 time steps with a step length of 1. The time allowed almost all (>99.9%) of the simulated communities to recover fully (Supplementary Fig. 8). The simulations were performed in *R* version 3.2.4 (ref. [66]) using the 'deSolve' library[67] with the solver 'lsoda'.

Because predators tend to be particularly important drivers of community dynamics and stability[7,31–33], we examined the responses of our simulated communities to instantaneous reductions in the densities of the apex predator in the system. However, we also explored whether the effect of environmental stochasticity on stability and its uncertainty are sensitive to the identity of the species receiving the pulse perturbation by perturbing each of the four species of the diamond module in isolation (that is, module 2 in Supplementary Fig. 1). We found that the general effect of environmental autocorrelation on the response and predictability of the various dimensions of ecological stability we quantified is robust to the identity of the consumer species receiving perturbations, but that this was not the case for the basal species (Supplementary Fig. 9). Rather, the relatively high abundances and intrinsic growth rates of the basal species enabled them to compensate rapidly for the initial reduction in their population densities in perturbed communities. This resulted in the Euclidean distance of the perturbed community decreasing monotonically from its equilibrium immediately following the perturbation and, thus, the maximum distance between perturbed and unperturbed communities occurring at the point of perturbation itself. Because of this, the extent of community change caused by the perturbation was unaffected by the temporal autocorrelation of environmental stochasticity when the basal species was perturbed in isolation (Supplementary Fig. 9). Given this, our results may not extend to situations where a direct and isolated pulse perturbation is conducted on a species with an extremely rapid response and where there is barely time for short-term environmental structure to have any obvious impact.

The recovery time for each food-web simulation was quantified as the time when the difference between the 'unperturbed' and 'perturbed' community dynamics reduced to a critical level (Fig. 1b). This corresponded to the first time step when the difference between the densities of all species in the perturbed and unperturbed communities was less than 0.01, and this difference was maintained for at least 50 time steps thereafter to ensure convergence had been achieved. The maximum Euclidean distance between perturbed and unperturbed communities, which we measured at each simulation step, was used to measure resistance (Fig. 1c). Increases in Euclidian distance correspond to reductions in resistance, and vice versa[22]. We quantified variability as the standard deviation of the total density of the unperturbed community during the simulation time window divided by its mean (Fig. 1d). As variability is a function of time, we also explored how the duration of the time window over which it was quantified affects our measure of variability and its uncertainty. We therefore measured variability over both the entire time series of the simulations and during only the recovery period (that is, 'transient' variability). We found that both variability measures responded similarly to the temporal autocorrelation of environmental noise, although the uncertainty associated with transient variability was markedly higher than for when variability was measured over the entire time series (Supplementary Fig. 2). We report only the results of variability measured over the entire time series of the simulations in our analyses.

Random forest regression. We examined the capacity of environmental stochasticity and a range of community and module characteristics (see Fig. 5 for a full list of explanatory variables used in the models) to explain the responses of each of our three focal stability dimensions using random forest regression at two analytical scales. The first includes the data from across all of the individual replicate ($n = 50$) stochasticity regimes for each distinct community, and thus incorporates variation in the responses of food webs to distinct runs of environmental stochasticity (that is, the specific temporal responses of communities) described by autocorrelation and species response correlation, while the second omits the variation across these replicate stochasticity regimes to focus only on the mean stability response of each community for each stochasticity treatment combination, indicating the general response pattern at the level of each food web. The random forest algorithm converges on an optimal solution from individual solutions of multiple trees (500 regression trees in this case) using bootstrapping and is non-parametric, not subject to distributional assumptions, compatible with categorical, ordinal and continuous data simultaneously, invariant to outliers and monotonic transformations of variables, and capable of handling high-dimensional data and identifying and incorporating complex variable interactions[68,69]. Random forest regression was therefore appropriate for analysis of our multiple-layer dataset given the skewed distribution and nonlinear responses of many of our stability components (for example, Supplementary Fig. 8) and the need to include both continuous and categorical variables as predictors. The importance of each predictor in the random forest is computed from permuting out-of-bag data[70]. For each tree, the prediction (mean-squared) error on the out-of-bag portion of the data was recorded. The same was then done after permuting each of the predictors. The differences between the two were then averaged across all trees and normalized by the standard deviation of the differences. The random forest regression model was conducted in *R* version 3.2.4 (ref. [66]) using the 'ranger' library[71].

References

1. Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 365–377 (2012).
2. Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C. & Finnegan, S. Climate change and the past, present, and future of biotic interactions. *Science* **341**, 499–504 (2013).
3. Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B. & Wood, S. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783–786 (1998).
4. Oliver, T. H. et al. Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).
5. Petchey, O. L. et al. The ecological forecast horizon, and examples of its uses and determinants. *Ecol. Lett.* **18**, 597–611 (2015).
6. Urban, M. C. et al. Improving the forecast for biodiversity under climate change. *Science* **353**, aad8466 (2016).
7. Donohue, I. et al. Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. *Glob. Change Biol.* **23**, 2962–2972 (2017).
8. Thompson, R. M., Beardall, J., Beringer, J., Grace, M. & Sardina, P. Means and extremes: building variability into community-level climate change experiments. *Ecol. Lett.* **16**, 799–806 (2013).
9. Donohue, I. et al. Navigating the complexity of ecological stability. *Ecol. Lett.* **19**, 1172–1185 (2016).
10. Vellend, M. *The Theory of Ecological Communities* (Princeton Univ. Press, Princeton, NJ, USA, 2016).
11. Boettiger, C. From noise to knowledge: how randomness generates novel phenomena and reveals information. *Ecol. Lett.* **21**, 1255–1267 (2018).
12. Halley, J. M. Ecology, evolution and 1/f-noise. *Trends Ecol. Evol.* **11**, 33–37 (1996).
13. Ruokolainen, L., Linden, A., Kaitala, V. & Fowler, M. S. Ecological and evolutionary dynamics under coloured environmental variation. *Trends Ecol. Evol.* **24**, 555–563 (2009).
14. Vasseur, D. A. & Yodzis, P. The color of environmental noise. *Ecology* **85**, 1146–1152 (2004).
15. Easterling, D. R. et al. Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074 (2000).
16. Jentsch, A., Kreyling, J., Boettcher-Treschkow, J. & Beierkuhnlein, C. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. *Glob. Change Biol.* **15**, 837–849 (2009).
17. Kayler, Z. E. et al. Experiments to confront the environmental extremes of climate change. *Front. Ecol. Environ.* **13**, 219–225 (2015).
18. Kuparinen, A., Keith, D. M. & Hutchings, J. A. Increased environmentally driven recruitment variability decreases resilience to fishing and increases uncertainty of recovery. *ICES J. Mar. Sci.* **71**, 1507–1514 (2014).
19. Crone, E. E. Contrasting effects of spatial heterogeneity and environmental stochasticity on population dynamics of a perennial wildflower. *J. Ecol.* **104**, 281–291 (2016).
20. Fowler, M. S. & Ruokolainen, L. Colonization, covariance and colour: environmental and ecological drivers of diversity–stability relationships. *J. Theor. Biol.* **324**, 32–41 (2013).
21. Ruokolainen, L., Ranta, E., Kaitala, V. & Fowler, M. S. Community stability under different correlation structures of species' environmental responses. *J. Theor. Biol.* **261**, 379–387 (2009).
22. Donohue, I. et al. On the dimensionality of ecological stability. *Ecol. Lett.* **16**, 421–429 (2013).
23. Pimm, S. L. The complexity and stability of ecosystems. *Nature* **307**, 321–326 (1984).
24. Ives, A. R. & Carpenter, S. R. Stability and diversity of ecosystems. *Science* **317**, 58–62 (2007).
25. May, R. M. *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, NJ, USA, 1973).
26. Sabo, J. L. & Post, D. M. Quantifying periodic, stochastic, and catastrophic environmental variation. *Ecol. Monogr.* **78**, 19–40 (2008).
27. Pimm, S. L. & Lawton, J. H. Number of trophic levels in ecological communities. *Nature* **268**, 329–331 (1977).

28. Pimm, S. L. & Lawton, J. H. On feeding on more than one trophic level. *Nature* **275**, 542–544 (1978).

29. Petchey, O. L., Eklof, A., Borrvall, C. & Ebenman, B. Trophically unique species are vulnerable to cascading extinction. *Am. Nat.* **171**, 568–579 (2008).

30. Ruokolainen, L. & Fowler, M. S. Community extinction patterns in coloured environments. *Proc. R. Soc. B* **275**, 1775–1783 (2008).

31. Estes, J. A. et al. Trophic downgrading of planet Earth. *Science* **333**, 301–306 (2011).

32. O'Connor, N. E., Emmerson, M. C., Crowe, T. P. & Donohue, I. Distinguishing between direct and indirect effects of predators in complex ecosystems. *J. Anim. Ecol.* **82**, 438–448 (2013).

33. White, L., Donohue, I., Emmerson, M. C. & O'Connor, N. E. Combined effects of warming and nutrients on marine communities are moderated by predators and vary across functional groups. *Glob. Change Biol.* **24**, 5853–5866 (2018).

34. Bascompte, J. & Melian, C. J. Simple trophic modules for complex food webs. *Ecology* **86**, 2868–2873 (2005).

35. Kondoh, M. Building trophic modules into a persistent food web. *Proc. Natl Acad. Sci. USA* **105**, 16631–16635 (2008).

36. Milo, R. et al. Network motifs: simple building blocks of complex networks. *Science* **298**, 824–827 (2002).

37. Clark, J. S. Uncertainty and variability in demography and population growth: a hierarchical approach. *Ecology* **84**, 1370–1381 (2003).

38. Clark, J. S. Individuals and the variation needed for high species diversity in forest trees. *Science* **327**, 1129–1132 (2010).

39. Laakso, J., Kaitala, V. & Ranta, E. Non-linear biological responses to environmental noise affect population extinction risk. *Oikos* **104**, 142–148 (2004).

40. Ripa, J. & Heino, M. Linear analysis solves two puzzles in population dynamics: the route to extinction and extinction in coloured environments. *Ecol. Lett.* **2**, 219–222 (1999).

41. Loreau, M. & de Mazancourt, C. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett.* **16**, 106–115 (2013).

42. Tilman, D. Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350–363 (1996).

43. Wang, S. P. & Loreau, M. Biodiversity and ecosystem stability across scales in metacommunities. *Ecol. Lett.* **19**, 510–518 (2016).

44. Ives, A. R., Gross, K. & Klug, J. L. Stability and variability in competitive communities. *Science* **286**, 542–544 (1999).

45. Kalinkat, G. et al. Body masses, functional responses and predator–prey stability. *Ecol. Lett.* **16**, 1126–1134 (2013).

46. Kaneryd, L. et al. Species-rich ecosystems are vulnerable to cascading extinctions in an increasingly variable world. *Ecol. Evol.* **2**, 858–874 (2012).

47. Berlow, E. L. et al. Simple prediction of interaction strengths in complex food webs. *Proc. Natl Acad. Sci. USA* **106**, 187–191 (2009).

48. Van der Bolt, B., van Nes, E. H., Bathiany, S., Vollebregt, M. E. & Scheffer, M. Climate reddening increases the chance of critical transitions. *Nat. Clim. Change* **8**, 478–484 (2018).

49. Scheffer, M. et al. Early-warning signals for critical transitions. *Nature* **461**, 53–59 (2009).

50. Greenman, J. V. & Benton, T. G. The amplification of environmental noise in population models: causes and consequences. *Am. Nat.* **161**, 225–239 (2003).

51. Murdoch, W. M., Briggs, C. J. & Nisbet, R. M. *Consumer–Resource Dynamics* (Princeton Univ. Press, Princeton, NJ, USA, 2003).

52. Mayfield, M. M. & Stouffer, D. B. Higher-order interactions capture unexplained complexity in diverse communities. *Nat. Ecol. Evol.* **1**, 0062 (2017).

53. Cohen, J. E., Jonsson, T. & Carpenter, S. R. Ecological community description using the food web, species abundance, and body size. *Proc. Natl Acad. Sci. USA* **100**, 1781–1786 (2003).

54. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).

55. Healy, K. et al. Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc. R. Soc. B* **281**, 20140298 (2014).

56. Paine, R. T. Food-web analysis through field measurement of per-capita interaction strength. *Nature* **355**, 73–75 (1992).

57. Wootton, J. T. & Emmerson, M. Measurement of interaction strength in nature. *Annu. Rev. Ecol. Evol. Syst.* **36**, 419–444 (2005).

58. Emmerson, M. & Yearsley, J. M. Weak interactions, omnivory and emergent food-web properties. *Proc. R. Soc. B* **271**, 397–405 (2004).

59. Gilpin, M. E. Stability of feasible predator–prey systems. *Nature* **254**, 137–139 (1975).

60. Jansen, V. A. A. & Kokkoris, G. D. Complexity and stability revisited. *Ecol. Lett.* **6**, 498–502 (2003).

61. Heino, M., Ripa, J. & Kaitala, V. Extinction risk under coloured environmental noise. *Ecography* **23**, 177–184 (2000).

62. Greenman, J. V. & Benton, T. G. The impact of environmental fluctuations on structured discrete time population models: resonance, synchrony and threshold behaviour. *Theor. Popul. Biol.* **68**, 217–235 (2005).

63. Fowler, M. S. & Ruokolainen, L. Confounding environmental colour and distribution shape leads to underestimation of population extinction risk. *PLoS ONE* **8**, e55855 (2013).

64. Cohen, J. E., Newman, C. M., Cohen, A. E., Petchey, O. L. & Gonzalez, A. Spectral mimicry: a method of synthesizing matching time series with different Fourier spectra. *Circ. Syst. Signal Process.* **18**, 431–442 (1999).

65. Ruokolainen, L., Fowler, M. S. & Ranta, E. Extinctions in competitive communities forced by coloured environmental variation. *Oikos* **116**, 439–448 (2007).

66. R Development Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2016).

67. Soetaert, K., Petzoldt, T. & Setzer, R. W. Solving differential equations in R: package deSolve. *J. Stat. Softw.* **33**, 1–25 (2010).

68. Evans, J. S., Murphy, M. A., Holden, Z. A. & Cushman, S. A. in *Predictive Species and Habitat Modeling in Landscape Ecology* (eds. Drew, C. A., Wiersma, Y. & Huettmann, F.) 139–159 (Springer-Verlag, New York, 2011).

69. Shi, T. & Horvath, S. Unsupervised learning with random forest predictors. *J. Comput. Graph. Stat.* **15**, 118–138 (2006).

70. Liaw, A. & Wiener, M. Classification and regression by randomForest. *R News* **2**, 18–22 (2002).

71. Wright, M. N. & Ziegler, A. ranger: a fast implementation of random forests for high dimensional data in C++ and R. *J. Stat. Softw.* **77**, 1–17 (2017).

Author contributions

Q.Y., I.D., A.L.J. and M.S.F. designed the research. Q.Y. performed the numerical simulations and analysed the data. Q.Y. and I.D. drafted the text. All authors contributed to writing the manuscript.

Competing interests

The authors declare no competing interests.

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Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	This study involved extensive simulations of food-web dynamics in the stochastic environment. The simulation was mainly accomplished by the Lonsdale system - a high performance compute cluster hosted and managed in Trinity College Dublin - using R version 3.2.4 with the R package 'deSolve'.
Data analysis	The main data analysis, random forest regression model, was conducted in R version 3.2.4 using the 'ranger' library.

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All core data including the constructed communities, time series of environmental stochasticity, and ecological stabilities, and the R codes for generating the results and figures of this paper are available at https://github.com/qiang-yang-ecology/Yang.et.al.stochasticity.stability.NEE.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	In this study, we explored how the three key components of ecological stability - recovery time, the extent of change, and variability - are regulated by environmental stochasticity. Specifically, we used simulated model food-webs described by the general Lotka-Volterra system to examine both the nature and predictability of these stability responses along gradients of two key factors that characterize stochasticity - its temporal autocorrelation and the correlations in species responses to it.
Research sample	The research data of this study was generated by simulating food-web dynamics in silico. We constructed 100 individual communities within each set of 14 different module structures and simulated their dynamics within a range of regimes of environmental stochasticity within a fully-crossed design using the environmental autocorrelation (5 gradients) and the correlations in species responses to it (3 gradients).
Sampling strategy	We constructed multiple communities with the parameter values randomly sampled from the reasonable biological and ecological range. The designed stochasticity regimes covered a large range of environmental stochasticity.
Data collection	The research data of this study was generated by simulating food-web dynamics with high-performance computer Lonsdale in Trinity College Dublin.
Timing and spatial scale	The simulation started in April 2017 and was finished in June 2017. The spatial scale is not applicable to the simulation in this study.
Data exclusions	For a simulation of the perturbed community, if it has not recovered to its equilibrium until the 1000th simulation time step with a step length of 1, the simulation is terminated. With this standard, less than 0.1% of all simulations were terminated.
Reproducibility	All R codes producing the original simulation data, quantifying ecological stability components, and analyzing the stability data were preserved in R Markdown file for reproducibility. We compiled our R codes and the reproduced figures in a single html file (compiled by the R Markdown) to the GitHub repository https://github.com/qiang-yang-ecology/Yang.et.al.stochasticity.stability.NEE.
Randomization	The parameter values of the communities were randomly sampled from the reasonable biological and ecological range.
Blinding	Blinding was not relevant to our study.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	Unique biological materials
☒	Antibodies
☒	Eukaryotic cell lines
☒	Palaeontology
☒	Animals and other organisms
☒	Human research participants

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging