Modelling the effects of spatial connectivity on community stability in Western Riverside County

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Summary

Predicting the effects of changing spatial connectivity on community stability is a challenging but crucial objective for effective conservation in the present age of widespread human development and habitat fragmentation (Chen, Li, and Allen 2010; Crooks and Sanjayan 2006; Fahrig 2003). This goal is further complicated by the complex role of dispersal in driving community dynamics; while the importance of dispersal in maintaining diversity has been well demonstrated in the general case (Leibold et al. 2004; Marcel Holyoak, Leibold, and R. D. Holt 2005), its effects can vary dramatically given the connectivity of a given ecosystem. Furthermore, predicting these effects requires models which incorporate the interactions between species and are suitable for inferring dynamics, for which common approaches such as presence-absence modelling do not suffice (Ives and Carpenter 2007; Keith et al. 2008; Swab et al. 2012). With this in mind, we utilize an allometric consumer-resource model to predict the effects of the progressive changes in habitat connectivity proposed by the Western Riverside County Multi-Species Habitat Conservation Plan (WRC MSHCP) on the dynamics of local communities.

Allometric modelling utilizes ordinary differential equations parameterized based on inferences from the readily observable physiological traits of species, particularly their body size and metabolic type (Yodzis and Innes 1992). As a result these models can be parameterized relatively easily from field data (Brose, Williams, and Martinez 2006; Berlow et al. 2009; Otto, Rall, and Brose 2007) and are highly effective for generating realistic random communities with the same physiological constraints observed in nature. We use this approach to model the dynamics of realistic random communities distributed spatially and dispersing according to the connectivity structure proposed in the WRC MSHCP (Dudek 2003, Figure 1). We then permute this structure by removing linkages between core habitat patches and observe the effects on community persistence, finding that the removal of even a single dispersal linkage between communities can have dramatic effects on the ability of species to coexist. Critically, we also observe that species and communities close to extinction are the most sensitive to differences in the structure of connectivity, emphasizing the importance of spatial processes in promoting the coexistence of at-risk species. We find that these effects depend strongly on the community and species considered however. Finally, we illustrate how the removal of specific connections between patches proposed by the MSHCP affects the persistence of species in a sample of random communities. Our results heavily emphasize that the effects of changing spatial connectivity depends strongly on the species present and their interactions, and that further work is needed to predict how specific communities in Western Riverside County will respond. While this work represents an early attempt to apply an underutilized modelling approach to a new conservation issue, we believe our framework can be used to provide deep insights into the functioning of communities to better aid their management.

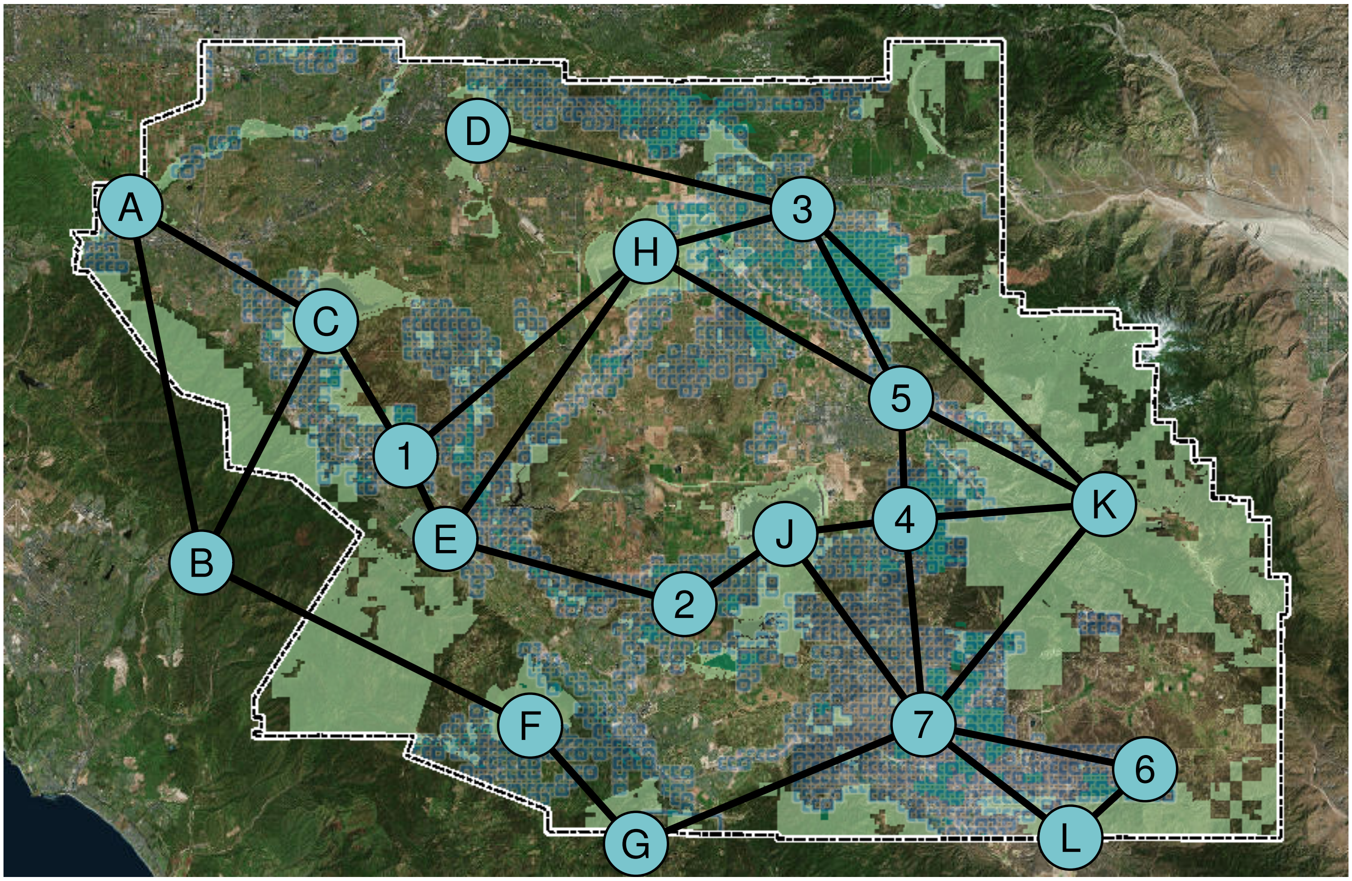

Figure 1: Representation of the connectivity structure used in the model overlaying the current GIS data for pre-existing (light green), newly acquired (dark green), and planned (blue) conserved lands under the WRC MSHCP (Dudek 2003). Labels correspond to the designations assigned by the MSHCP, where A-L correspond to existing and 1-7 to proposed core habitat patches. I was omitted from the model as it is not planned to connect with other patches, and M was merged with 7 given their high planned connectivity.

Methods

To model metacommunity dynamics we use an allometric consumer-resource model (Yodzis and Innes 1992) extended with dispersal and generalized for i species and p communities:

$$\frac{dB_{i,p}}{dt} = F(B_{i,p}) + G(B_{i,p}) - H(B_{i,p}) - I(B_{i,p}) + J(B_{i,p}) \tag{1}$$

$$F(B_{i,p}) = B_{i,p} a_{r,i} M_i^{-.25} (1 - \frac{B_{i,p}}{K_{i,p}\phi_p}) \tag{2}$$

$$G(B_{i,p}) = B_{i,p} a_{x,i} M_i^{-.25} \frac{\sum_{j=1} \omega_{i,j} B_{j,p}^h}{(B_0\phi_p)^h + \sum_{j=1} \omega i, j B_{j,p}^h} \tag{3}$$

$$H(B_{i,p}) = \sum_{j=1} \frac{a_{x,j} y_j M_j^{-.25} \omega_{j,i} B_{i,p}^h B_{j,p}}{e_{j,i}[(B_0\phi_p)^h + \sum_{k=1} \omega_{j,k} B_{k,i}^h]} \tag{4}$$

$$I(B_{i,p}) = B_{i,p} a_{x,i} M_i^{-.25} \tag{5}$$

$$J(B_{i,p}) = m_i \sum_{q=1} A_{q,p} B_{q,p} \tag{6}$$

Patch	Area (mi^2)	ϕ
A	11010	4.40
B	71490	28.60
C	23710	9.48
D	2500	1.00
E	4300	1.72
F	8360	3.34
G	4500	1.80
H	20809	8.32
J	29050	11.62
K	149750	59.9
L	24750	9.90
1	7470	2.99
2	5050	2.02
3	24940	9.98
4	11890	4.76
5	3220	1.29
6	4290	1.72
7	60460	24.18

Link	Permuted	Length (mi)	Width (mi)	$A_{p,q}$
A↔B	Yes	1.48	1	.0227
A↔C	Yes	6.12	1	.0002
B↔C	Yes	1.12	1	.0326
B↔F		4.06	1	.0017
C↔1		0	1.52	.1515
D↔3	Yes	9.27	1	$9.41 * 10^{-6}$
E↔H	Yes	10.40	1	$3.04 * 10^{-6}$
E↔1		4.11	1	.0016
E↔2		10.23	1	$3.62 * 10^{-6}$
F↔G		5.59	1	.0004
G↔7	Yes	7.24	1	.0001
H↔1	Yes	7.09	1	.0001
H↔3		0	4.84	.4845
H↔5	Yes	5.64	1	.0004
J↔2	Yes	.72	1	.0486
J↔4	Yes	3.57	1	.0028
J↔7	Yes	3.46	1	.0031
K↔3		0	3.92	.3921
K↔4		0	5.55	.5554
K↔5		0	8.3	.8303
K↔7		0	3	.2997
L↔6		0	4.45	.4452
L↔7	Yes	0	2.22	.2217
3↔5	Yes	1.53	1	.0216
4↔5	Yes	3.48	1	.0031
4↔7	Yes	0	1.75	.1753
6↔7	Yes	3.43	1	.0032

Table 1: WRC MSHCP Core habitat size and linkage measurements (Dudek 2003) and their derived patch size ϕ and dispersal weight $A_{p,q}$ parameters. Patch size ϕ was determined by scaling the area of each patch by the smallest (D), and $A_{p,q}$ as $.1(link\ width)e^{-(link\ length)}$.

Here the function F defines the primary production of a producer, G a consumers growth from consumption, H the biomass lost from predation, I the biomass lost from metabolic processes, and J the net flux in a population as a result of immigration and emigration. All species are either producers or consumers; for producers G and I are set to 0, and likewise F is set to 0 for consumers.

In this model $B_{i,p}$ is the biomass of species i in community p, M its average body mass, and m its species-specific dispersal rate. For resource species, a_r is its mass-specific growth rate and K its carrying capacity. For consumer species, a_x is its mass-specific metabolic rate, y its maximum consumption rate relative to metabolic rate, $e_{i,j}$ its assimilation rate for species j. The functional response of consumers is defined by B_0, the half-saturation coefficient, and h, the shape parameter. Interactions between species (consumption) are defined by the matrix ω, where each element $\omega_{i,j}$ indicates the relative effort species j spends consuming species i; each column j sums to 1, the total effort each species has to allocate. Each patch has a size ϕ which scales K and B_0 from units of density to total biomass. Interactions between communities (dispersal) are defined by the matrix A, where each element $A_{p,q}$ indicates the strength of dispersal between community p and q relative to the species dispersal rate m_i. The diagonal elements $A_{p,p}$ are negative representing emigration and their values are such that $A_{p,p}$ (emigration) $+A_{p,\cdot}$ (immigration) $= 0$.

We generated a series of random but realistic communities to test the effects of changing connectivity structure in Western Riverside Country across a range of ecological contexts. Interactions between species ω were specified according to the niche model (Williams and Martinez 2000), and species' body mass M were inferred based on their trophic position following the methods of Brose, Williams, and Martinez 2006. The remaining species parameters depend primarily upon the metabolic type and feeding habits of species for which values have been well established (Yodzis and Innes 1992; Brose, Williams, and Martinez 2006; Lin and Sutherland 2013). To reduce the initial complexity of the model these values were set equal for all species, $a_x = .88, y = 4, e = .65$, corresponding to a community of omnivorous vertebrate ectotherms. In this model the values of biomass $B_{i,p}$ are relative to carrying capacity K and patch size ϕ; with this in mind K was set to 1, thus $B_{i,p}$ is a unitless proportion of carrying capacity K times patch size ϕ. Similarly, time is relative to the mass-specific productivity a_r which was set to 1. To promote oscillations the functional response was set to type II for all species ($B_0 = .5, h = 1$). The limit cycles a type II functional response is prone to are highly sensitive to the stabilizing effects of dispersal and emphasize the effects of changing connectivity on the community.

The number, arrangement, and connections between core habitat patches in the model (Figure 1) were derived from the goals of the WRC MSHCP (Dudek 2003, Table 1). As the model is not sensitive to absolute but rather relative differences in size and arrangement, patch size ϕ was expressed in the model as size relative to the smallest patch. In the model, the strength of a link between two patches $A_{p,q}$ is the proportion of the maximum dispersal rate m each link provides. The relative strength of each link is estimated by assuming dispersal decreases exponentially with link length and increases linearly with link width, with the ultimate effect being approximated by $.1 * (link\ width) e^{-(link\ length)}$ (Neubert, Kot, and Lewis 1995; Johst, Brandl, and Eber 2002). The scaling of these links means that the maximum dispersal rate m is the proportion of biomass exchanged between two adjacent patches with a 10 mi link ($link\ length = 0, link\ width = 10, A_{p,q} = 1$). To reduce initial model complexity m was held constant for all species, and set to .001. From this structure we derived alternatives by selectively removing proposed links and comparing dynamics between the plans full connectivity and our reduced alternatives.

For each combination of community, structure, and extinction threshold parameters 20 replicate simulations with random initial conditions were run. Random initial conditions were uniformly distributed on the interval $[.9, 1.1]$. This is the only source of stochastic variation in our model and is introduced to infer the effects of stochasticity observed in nature (demographic and/or environmental) on communities across the range of connectivity. Effects of connectivity structure on community dynamics across simulations were measured primarily in terms of feasibility, which requires that biomass $B_{i,p}$ is above a certain threshold in at least one patch p for all species i at all times. Higher threshold values approximate the extinction risk posed by higher rates of demographic or environmental stochasticity, which these deterministic models do not include otherwise. Unless otherwise stated, the threshold for feasibility used was $1 * 10^{-10}$ which represents very low extinction risk, allowing populations to reach very small numbers and still recover. We primarily report the proportion of simulations which are feasible out of all replicates. The minimum, average, and standard deviation of species biomass were also calculated to characterize the effects of spatial connectivity on overall population size and variability.

Results

We first observe the effects of removing connectivity links on a sample of food webs across a range of extinction thresholds (Figure 2). The observed food webs only respond to changes in spatial connectivity when the extinction threshold is within a certain range; when the feasibility threshold is too high or too low, communities are non-feasible or feasible in all treatments. At the range between these two extremes a community may be feasible or non-feasible depending on initial conditions. Such a community contains at least one species which is capable of persisting at a given

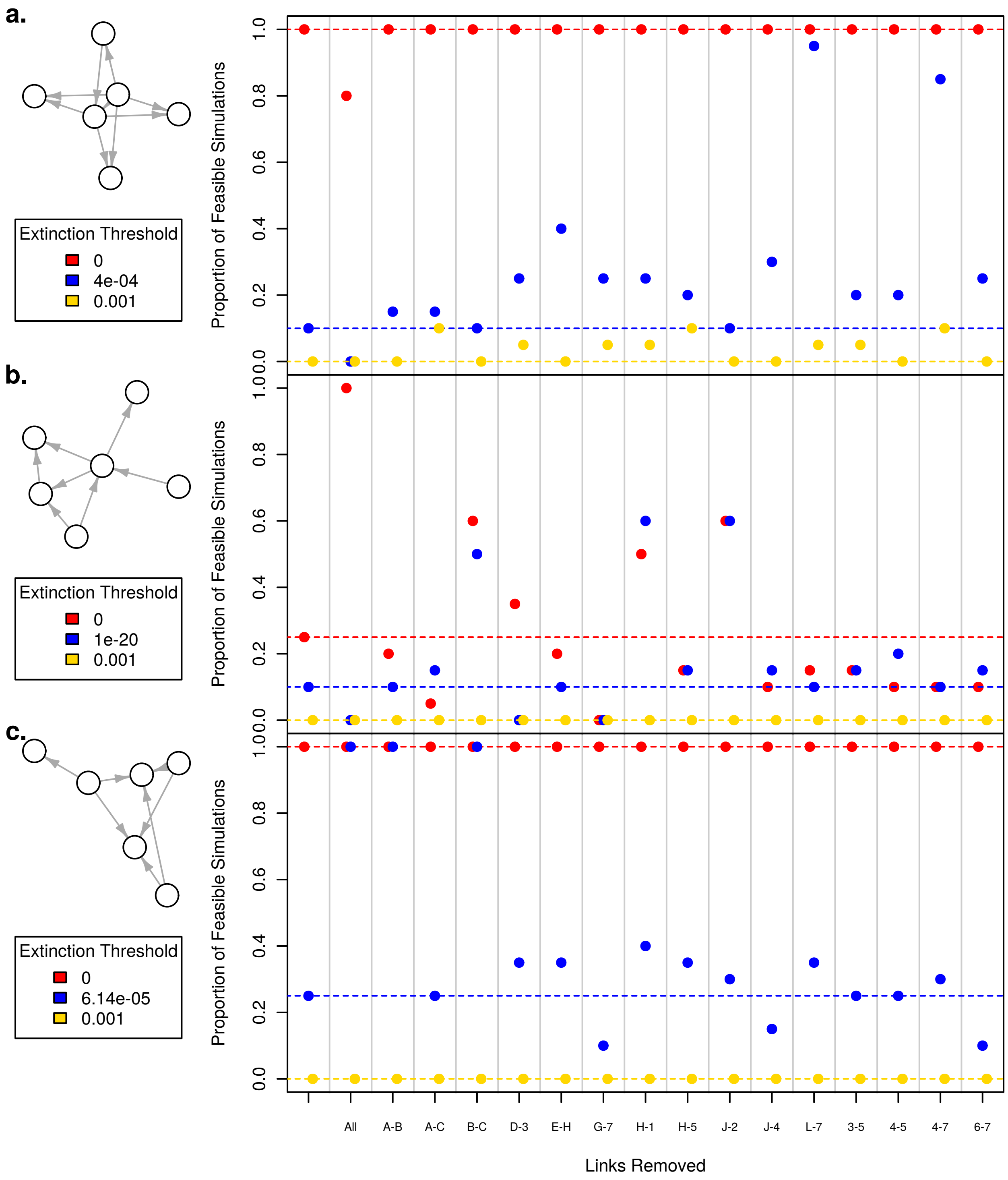

Figure 2: The effects of removing links between core habitat patches for three food webs at three levels of feasibility thresholds. The thresholds 0 and 0.001 were used as extreme values for all webs, with 0 being the minimum possible feasiblity threshold, allowing population sizes to become arbitrarily small and persist, and .001 a high enough threshold that persistence was rare or impossible for all food webs. Intermediate values with variable feasibility were then found for all food webs. All removals are compared to the full plan proposed by the MSHCP (dotted line, no removals) as a baseline.

threshold, but which may become extinct due to stochasticity. In this range substantial differences in the proportion of feasible simulations emerge between connectivity structures, suggesting that some patterns of spatial connectivity are better at mitigating the extinction risk of certain species.

The results of our simulations show a wide range of responses to the removal of proposed connections, but no clear agreement between food webs. This suggests strongly both the importance of connectivity in influencing the persistence of food webs and the high sensitivity to context. In Fig. 2, removing the connections between patches *L* and *7* or *4* and *7* leads to a large increase in feasibility for food web *a* but only a marginal increase *c*, while *b* shows no effect at all. Furthermore, removing all connections, effectively isolating all patches, has a positive effect for *c* but reduces the persistence of *a* even when the extinction threshold is at its absolute minimum. Meanwhile the persistence of *b* is increased by removing all connections when the extinction threshold is 0, but decreased when the extinction threshold increases. These results clearly cannot be readily generalized between species and communities and rather must be taken on a case-by-case basis until the mechanisms underlying these differences are better understood.

To further explore these effects we illustrate the dynamics of each species in Food web *b* from Fig. 2 in Figure 3. For species *a, c, d,* and *e* changing connectivity does not affect qualitative dynamics in a noticeable way, but nevertheless influences the regional variability of biomass. In this food web species *b* is most prone to extinction, and connectivity can be seen to strongly influence its average regional biomass and variability as well as that of its predator, species *f*. Moreover, it produces clear qualitative changes in the cycles of biomass, principally by influencing the timing of cycles relative to each patch. When the connection between patches *H* and *1* is removed species *b's* dynamics shift from a series of sporadic peaks in abundance to a set of two major peaks, consisting of a synchronized increase first in patches *J, K, L, 3 4, 5, 6,* and *7* followed by *A, B, C,* and *1,* with several minor peaks from *D, E, F, G, H,* and *2* in between. Species *f* is similarly affected, particularly in how closely peaks in abundance in patches close to patch *B* follow those close to *K*. Overall it appears that the effect of connectivity is strongest among species with periods of low abundance in some or all patches such as *b* and *f*, as dispersal becomes increasingly important to maintain both local and regional persistence.

In addition to illustrating significant differences between species' responses to changes in connectivity, these examples show that the effects of connectivity on species persistence are complex. While the proportion of feasible simulations is higher for food web *b* when the link between patches *H* and *1* is removed, other important properties of the species' dynamics are negatively affected (Table 2), an expected effect of increased synchrony between population cycles (Gouhier, Guichard, and Gonzalez 2010; Vandermeer 2006). Surprisingly, the minimum biomass is much lower suggesting that while species are more likely to persist in this case, they maintain populations much closer to extinction. Thus, while removing the link between *H* and *1* allows species *b* to reach a viable population size more consistently than the full connectivity proposed by the MSHCP, the species would likely be more at risk. Including a more complete representation of demographic and/or environmental stochasticity in our modelling framework and sampling over a wider range of feasibility thresholds would better capture these effects.

Link Removed	Average Biomass	S.D. of Biomass	Minimum Biomass
None	30.05	53.93	$3.90 * 10^{-6}$
A ↔B	36.14	76.21	$3.34 * 10^{-6}$
H ↔1	56.08	145.72	$6.59 * 10^{-16}$

Table 2: Summary statistics for species *b* from Figure 3.

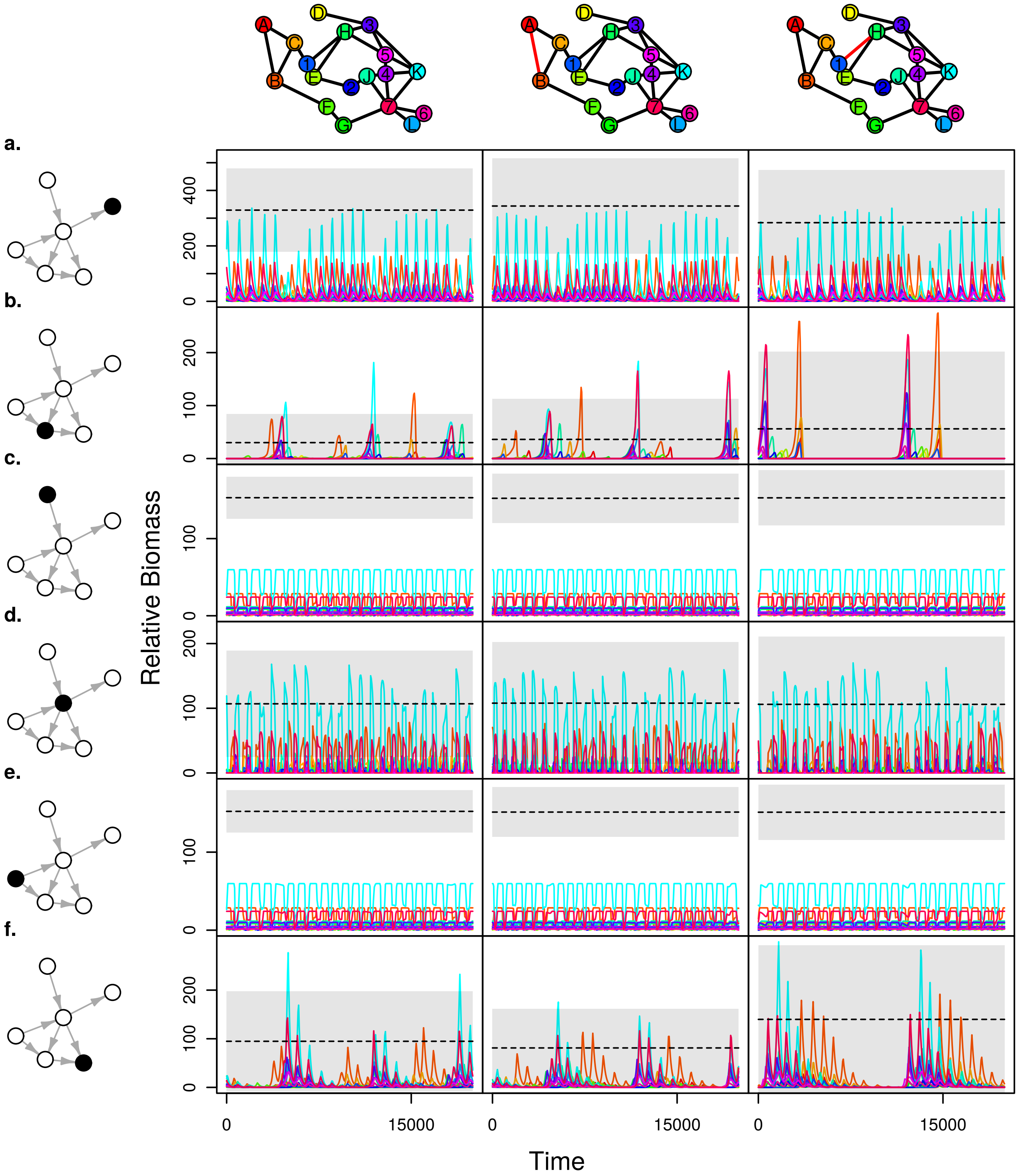

Figure 3: Example time series for each species from food web b., Figure 2. For connectivity graphs, the link in red was removed for a given simulation and the color of each core habitat patch is a key for differentiating each time series. For food web graphs, black indicates the focal species. Mean (dotted lines) and standard deviation (shaded grey) of regional biomass was calculated for each species.

Conclusion

Our results primarily demonstrate the enormous challenges inherent in predicting the effects of changing connectivity on community dynamics and persistence. As they are, our results provide suggestions to optimise the connectivity of Western Riverside County for the persistence of a selection of simplified food webs, with physiological parameters based on a community of omnivorous vertebrate ectotherms. From Figure 2, removing the connection between core habitat patches L and *7* best promotes persistence for food web a, removing the connection between H and *1* or J and *2* best promotes persistence for food web b, and removing connections between A and B, A and C, or all connections best promotes persistence for food web c. As these recommendations vary widely between food webs, further work including communities built from the biota of Western Riverside County are necessary before applying our results to the MSHCP. Much of the data necessary to parameterize the allometric model for these communities is readily available, although determining the structure of interactions between species remains a necessary challenge to overcome.

Though we caution against their direct application, our results do illustrate important points about the complexity of species' responses to changing connectivity. Even subtle changes in the connectivity of the MSHCP led to dramatic changes in the patterns of synchrony among patches and altered the ability of species to persist. In the case of food web b from Figure 2, removing a link between patches counter-intuitively increased synchrony among patches for species b, increased feasibility, but reduced the population minimum. Even in this relatively simple example with only six interacting species, community dynamics become incredibly complex and require a great deal more study to fully understand. Rather than having a single positive or negative effect, changing patterns of connectivity between communities in our model has many contrasting effects, the net effect of which will depend dramatically on the precise ecological context of each species.

As a first attempt at modelling the dynamics of an overwhelmingly complex system, our model has many limitations and opportunities for improvement. In addition to parameterizing communities from data on the biota of Western Riverside County, more realistic incorporation of demographic and environmental stochasticity is necessary to generate more effective predictions of the effects of connectivity, especially given the aforementioned complexity of these effects. We also used only a very basic representation of the spatial characteristics of the the MSHCP's proposed areas, and further iterations of our modelling framework should capture differences in habitat quality by varying carrying capacity K, rather than scaling by patch size alone. Our model also assumed equal dispersal among all species, and assumed all species could only disperse along specified corridors. Incorporating the differences in dispersal ability among species is clearly very important to accurately predict how a community will respond to changes in connectivity which ultimately are felt through their effect on species dispersal.

Overall we hope our modelling approach has demonstrated the importance of incorporating interactions between species and their dynamics for predicting the response of communities to changes in connectivity between core habitat patches. Though incomplete, we believe our framework provides a useful starting point for better understanding how connectivity influences community dynamics in nature and determining how these features enhance or constrain species' abilities to persist.

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