# *Modeling metapopulation in dynamic landscapes: toward a unified concept of temporal metapopulation capacity*

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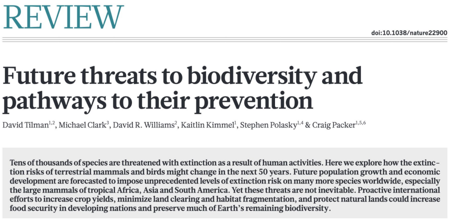
June 18, 2026

# Habitat loss: A critical threat to biodiversity



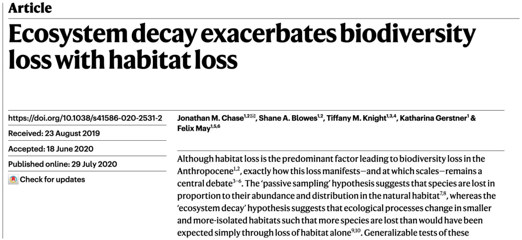
REVIEW

doi:10.1038/nature22900

## Future threats to biodiversity and pathways to their prevention

David Tilman[1,2], Michael Clark[3], David R. Williams[2], Kaitlin Kimmel[1], Stephen Polasky[1,4] & Craig Packer[1,5,6]

Tens of thousands of species are threatened with extinction as a result of human activities. Here we explore how the extinction risks of terrestrial mammals and birds might change in the next 50 years. Future population growth and economic development are forecasted to impose unprecedented levels of extinction risk on many more species worldwide, especially the large mammals of tropical Africa, Asia and South America. Yet these threats are not inevitable. Proactive international efforts to increase crop yields, minimize land clearing and habitat fragmentation, and protect natural lands could increase food security in developing nations and preserve much of Earth's remaining biodiversity.



Article

## Ecosystem decay exacerbates biodiversity loss with habitat loss

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Check for updates

Jonathan M. Chase[1,2]✉, Shane A. Blowes[1,2], Tiffany M. Knight[1,3,4], Katharina Gerstner[1] & Felix May[1,5,6]

Although habitat loss is the predominant factor leading to biodiversity loss in the Anthropocene[1,2], exactly how this loss manifests—and at which scales—remains a central debate[3–6]. The 'passive sampling' hypothesis suggests that species are lost in proportion to their abundance and distribution in the natural habitat[7,8], whereas the 'ecosystem decay' hypothesis suggests that ecological processes change in smaller and more-isolated habitats such that more species are lost than would have been expected simply through loss of habitat alone[9,10]. Generalizable tests of these

RESEARCH ARTICLE

APPLIED ECOLOGY

## Habitat fragmentation and its lasting impact on Earth's ecosystems

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Nick M. Haddad,[1]* Lars A. Brudvig,[2] Jean Clobert,[3] Kendi F. Davies,[4] Andrew Gonzalez,[5] Robert D. Holt,[6] Thomas E. Lovejoy,[7] Joseph O. Sexton,[8] Mike P. Austin,[9] Cathy D. Collins,[10] William M. Cook,[11] Ellen I. Damschen,[12] Robert M. Ewers,[13] Bryan L. Foster,[14] Clinton N. Jenkins,[15] Andrew J. King,[9] William F. Laurance,[16] Douglas J. Levey,[17] Chris R. Margules,[18,19] Brett A. Melbourne,[4] A. O. Nicholls,[9,20] John L. Orrock,[12] Dan-Xia Song,[8] John R. Townshend[8]

Article

## Species turnover does not rescue biodiversity in fragmented landscapes

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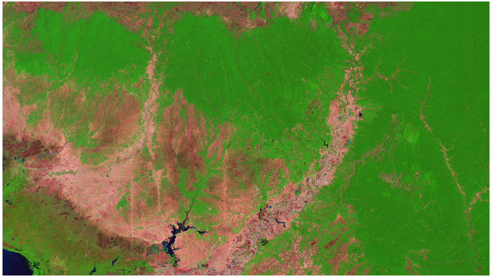
Thiago Gonçalves-Souza[1,2]✉, Jonathan M. Chase[3,4], Nick M. Haddad[5], Maurício H. Vancine[6], Raphael K. Didham[7,8], Felipe L. P. Melo[9,10], Marcelo A. Aizen[11], Enrico Bernard[12], Adriano G. Chiarello[13], Deborah Faria[14], Heloise Gibb[15], Marcelo G. de Lima[16,17], Luiz F. S. Magnago[18], Eduardo Mariano-Neto[19], André A. Nogueira[20], André Nemésio[21], Marcelo Passamani[22], Bruno X. Pinho[23], Larissa Rocha-Santos[14], Rodolpho C. Rodrigues[24], Nathalia Vieira Hissa Safar[18], Bráulio A. Santos[25], Alejandra Soto-Werschitz[26], Marcelo Tabarelli[7], Marcio Uehara-Prado[27], Heraldo L. Vasconcelos[21], Simone Vieira[28] & Nathan J. Sanders[2]

# *Temporal connectivity*

### 1. Habitat degradation

- Caused by both natural phenomena and land-use change by humans.
- Leads to habitat loss and altered ecosystem processes.



Forest in Cambodia – February 20, 1999 (NASA)

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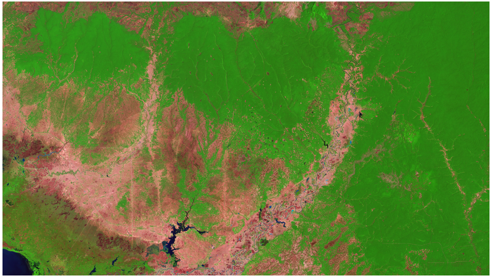
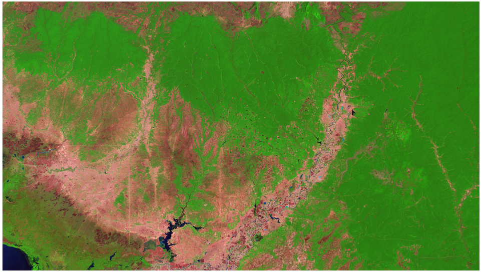


Forest in Cambodia – February 20, 1999 (NASA)

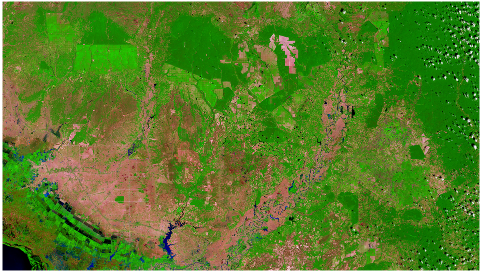
## 2. Seasonal fragmentation

- Some species rely on seasonally available habitats (e.g., wetlands, meadows).
- Migration becomes essential for survival and reproduction.

# *A world of fragmented habitats and temporal variations*



*(a)* February 20, 1999

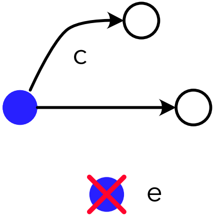


*(b)* February 5, 2017

**Impacts of temporal habitat variations:**

- Influence species persistence.
- Affect the movement of individuals, diseases, and disturbances.

# Metapopulation: Levins model



Levins model[1] (1969): a simple model to explain the dynamic of a species in a patchy environment.

Call $p(t)$ the proportion of patches occupied by the species of interest at time $t$ and assume that

1. an empty patch is colonized by the populations in other patches with rate $cp(t)$ where $c$ is the colonization rate,
2. that occupied patches become empty at rate $e$ where $e$ is the extinction rate.

The proportion of patches occupied by the population at time $t$ is:

$$\frac{dp(t)}{dt} = cp(t)(1 - p(t)) - ep(t)\,.$$

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[1] Levins (1969), *Bulletin of the Entomological Society of America*, **15-3**, 237–240

# A network of 56 habitat patches

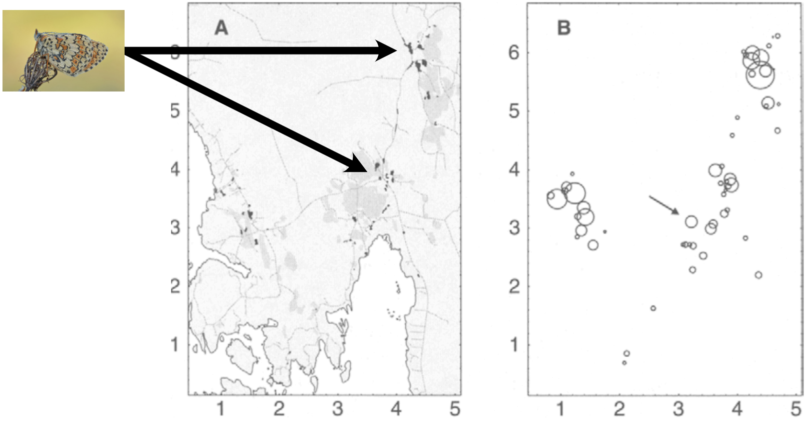

*Figure 2:* Glanville fritillary butterfly (Melitaea cinxia) in the Åland Islands in Finland.

Hanski (1999), *Metapopulation Ecology*, OUP Oxford

# *Spatially realistic metapopulation model*

$$\frac{dp_k(t)}{dt} = c_k(\boldsymbol{p})(1 - p_k(t)) - e_k(\boldsymbol{p})p_k(t), \quad \forall k \in [n],$$

where $p_k(t)$ is the probability that patch $k$ is occupied at time $t$.

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**Colonization rate of an empty patch $k$:**

$$c_k(\boldsymbol{p}) = c \sum_{\ell \neq k} A_\ell f(d_{k\ell}) p_\ell\,,$$

where:

| | |
|---|---|
| $c$ | colonization rate, |
| $f$ | kernel function, |
| $d_{k\ell}$ | distance between patches $k$ and $\ell$, |
| $A_\ell$ | area of patch $\ell$. |

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**Extinction rate of patch $k$:**

$$e_k(\boldsymbol{p}) = e/A_k,$$

where:

| | |
|---|---|
| $e$ | extinction rate, |
| $A_k$ | area of patch $k$. |

Hanski & Ovaskainen (2000) *Nature* **404**, 755–758

# *Dynamics of the metapopulation model*

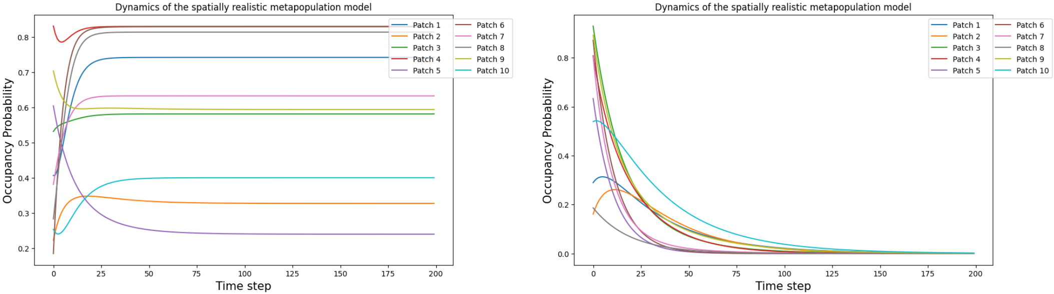

*Figure 3:* Dynamics of the metapopulation model for 10 patches and 2 different connectivity matrices.

# The metapopulation capacity

$$\begin{aligned}\frac{dp_k}{dt} &= (1-p_k)\, c \sum_{\ell \neq k} A_\ell f(d_{k\ell}) p_\ell - \frac{e}{A_k} p_k\,,\\ &= \frac{e}{A_k}\left((1-p_k)\frac{c}{e}(M\boldsymbol{p})_k - p_k\right)\,,\end{aligned}$$

where $M_{k\ell} = A_k A_\ell f(d_{k\ell})$, $k \neq \ell$ and $M_{kk} = 0$, $\forall k \in [n]$, known as the landscape matrix.

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where $M_{k\ell} = A_k A_\ell f(d_{k\ell}),\ k \neq \ell$ and $M_{kk} = 0,\ \forall k \in [n]$, known as the landscape matrix.

The largest eigenvalue of $M$ determines the existence of a positive equilibrium $p_k(t) > 0$ as a threshold:

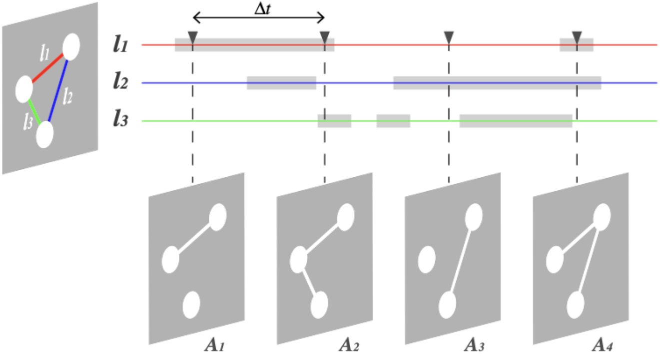
$$\lambda_M > \frac{e}{c}\,.$$

We call $\lambda_M$ **the metapopulation capacity**

Hanski & Ovaskainen (2000) *Nature* **404**, 755–758

# *Temporal networks*

Temporal networks: networks where connections between nodes can change over time.



Valdano *et al.* (2015), *Physical Review X*, **5**, 021005

# *Discrete and temporal metapopulation model*

**Microscopic Markov Chain model** (static landscape):

$$p_k(t+1) = 1 - [1 - (1 - e_k)p_k(t)] \prod_\ell [1 - cS_{\ell k} p_\ell(t)],$$

with $\boldsymbol{e} = (e/A_1, \ldots, e/A_n)$ and $S_{k\ell} = A_k f(d_{k\ell})$.

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**Temporal model:** let $A_k^{(t)}$ and $d_{k\ell}^{(t)}$ vary in time, so $e_k^{(t)} = e/A_k^{(t)}$ and $S_{k\ell}^{(t)} = A_k^{(t)} f(d_{k\ell}^{(t)})$. The dynamics become

$$p_k(t+1) = 1 - \left[1-(1-e_k^{(t)})p_k(t)\right] \prod_\ell \left[1 - cS_{\ell k}^{(t)}\, p_\ell(t)\right], \quad \forall k \in [n].$$

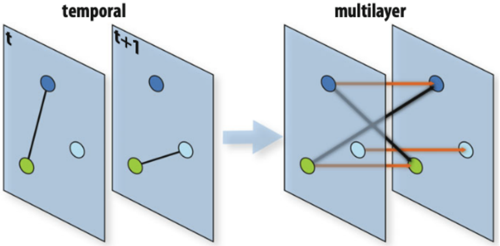
Gómez et al. (2010) *EPL* **89-3**, 38009 ; Granell et al. (2024) *Ann. Phys.* **536**, 2400078.

# Multilayer representation of temporal networks

Stacking the $T$ snapshots as a tensor network coupling colonization and extinction:

$$\hat{M}^{ts}_{k\ell} = \delta^{t,s+1}\left[(1 - e^{(t)}_k)\delta_{k\ell} + cS^{(t)}_{k\ell}\right], \qquad S^{(t)}_{k\ell} = A^{(t)}_k f(d^{(t)}_{k\ell}).$$

$\hat{M}$ encodes both processes and the landscape structure through time.



Valdano *et al.* (2015), *Physical Review X*, **5**, 021005

# *Supra-adjacency formulation and temporal capacity*

Mapping $(k, t) \mapsto \alpha = nt + k$ unrolls $\hat{M}$ into the $nT \times nT$ supra-adjacency matrix

$$\hat{M} = \begin{pmatrix} 0 & B^{(1)} & 0 & \cdots & 0 \\ 0 & 0 & B^{(2)} & \cdots & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & 0 & \cdots & B^{(T-1)} \\ B^{(T)} & 0 & 0 & \cdots & 0 \end{pmatrix}, \quad B^{(t)} = I - \mathrm{diag}(\boldsymbol{e}^{(t)}) + cS^{(t)}.$$

# Asymptotic behavior of the dynamical system

Let $\hat{\boldsymbol{p}}(\tau)$ of size $nT$ collect the occupation probabilities over one period $[\tau T, (\tau+1)T]$, with Markov dynamics

$$\hat{p}_\alpha(\tau+1) = 1 - \prod_{\beta}^{nT} \left[1 - \hat{M}_{\beta\alpha}\, \hat{p}_\beta(\tau)\right].$$

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Linearizing the $T$-periodic map around $\hat{\boldsymbol{p}}^* = 0$ yields

$$\hat{\boldsymbol{p}}(\tau+1) = \hat{M}\, \hat{\boldsymbol{p}}(\tau),$$

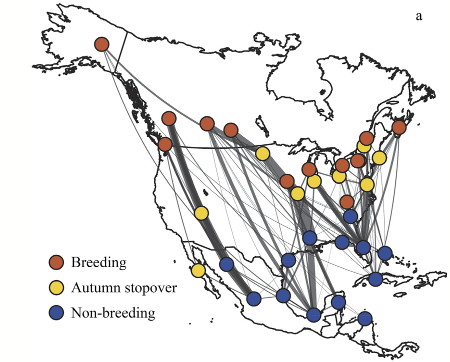
hence the metapopulation persists asymptotically if and only if

$$\rho(\hat{M}) > 1,$$

that we call **temporal metapopulation capacity.**

# *Motivation: Migratory network*

Migratory network for Tree Swallows showing breeding, autumn stopover, and non-breeding nodes:



*(a)* Migratory network

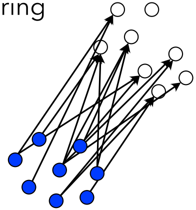
*(b)* A tree swallow

Knight *et al.* (2018), *Ecological Monographs*, **88-3**, 445–460

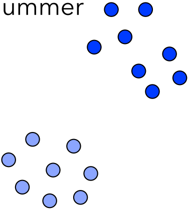
# *Toy model: Migratory network*

$$\begin{pmatrix} 0 & 0 \\ S_{\text{Winter}\to\text{Summer}} & 0 \end{pmatrix} \qquad \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix} \qquad \begin{pmatrix} 0 & S_{\text{Summer}\to\text{Winter}} \\ 0 & 0 \end{pmatrix} \qquad \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$$

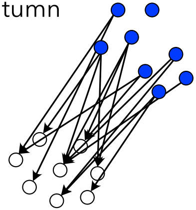
Spring



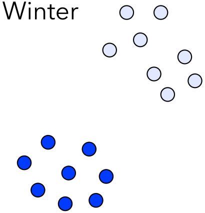
Summer



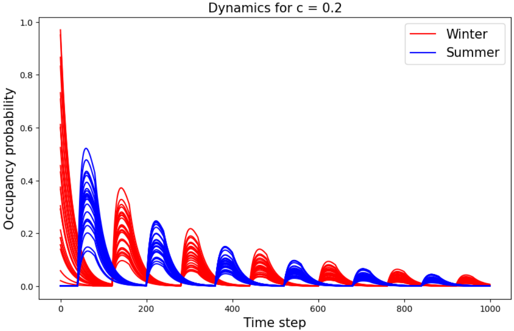
Autumn



Winter



# *Example: Migratory network*



*(a)* Colonization rate $c = 0.2$

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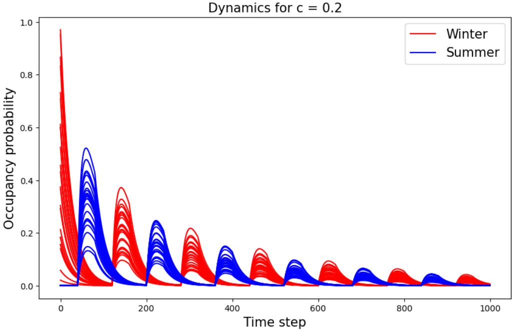
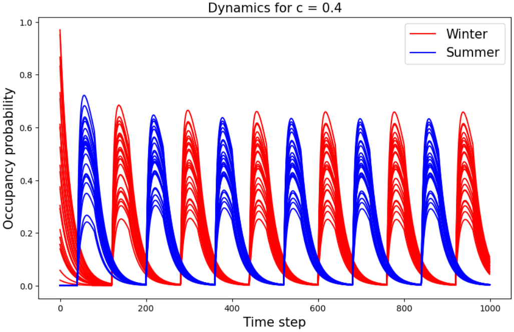
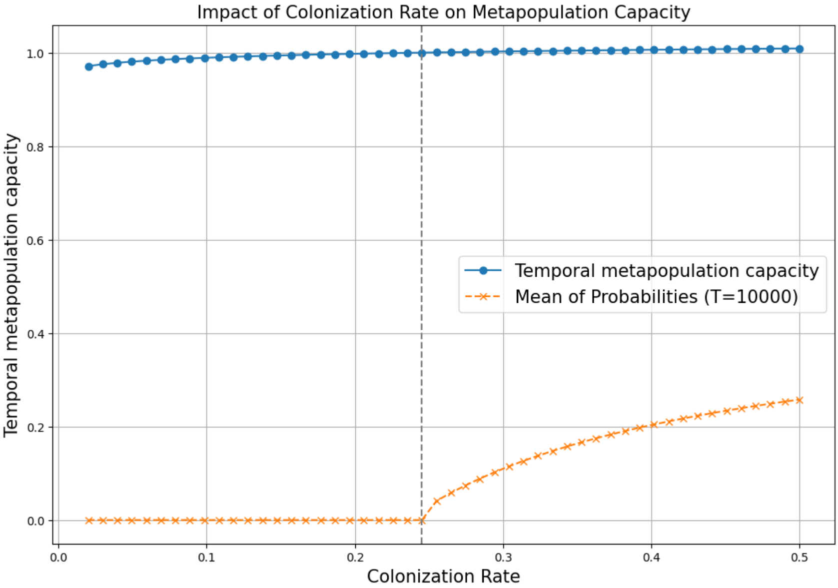


*(a)* Colonization rate $c = 0.2$



*(b)* Colonization rate $c = 0.4$

# *Example: Migratory network*



# *Take-Home Message*

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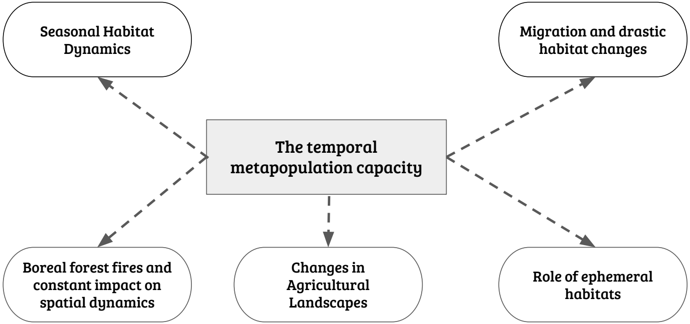
- Needs of **empirical and theoretical ecologists**.
- Develops a **theoretical framework** to quantify temporal dynamics of metapopulations, ensuring resilient ecosystems.
- New metric: the “**temporal metapopulation capacity**” to quantify the ability of a metapopulation to persist in a dynamically changing landscape.



# *Longer-term perspectives*

- Metacommunity ecology: Investigate how species interactions and dispersal shape community assembly and dynamics at multiple spatial scales.

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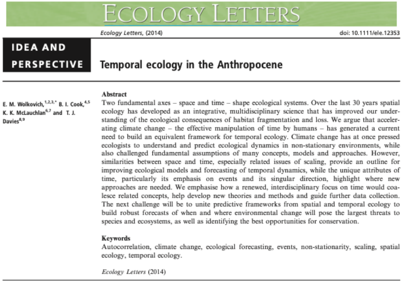
- Metacommunity ecology: Investigate how species interactions and dispersal shape community assembly and dynamics at multiple spatial scales.
- Time-varying interaction networks: Analyze how changes in species interactions over time influence ecological patterns and processes.

*“In the twentieth century, classical Newtownian physics gave way to Einstein’s theory of relativity with the recognition that time is not simply a fourth dimension orthogonal to space, but a relative metric, inherently intertwined with space. Ecology now has an opportunity to build a similarly integrative spatiotemporal framework.”*



ECOLOGY LETTERS

*Ecology Letters*, (2014) doi: 10.1111/ele.12353

**IDEA AND PERSPECTIVE**

**Temporal ecology in the Anthropocene**

E. M. Wolkovich,[1,2,3,*] B. I. Cook,[4,5] K. K. McLauchlan[6,7] and T. J. Davies[8,9]

**Abstract**

Two fundamental axes – space and time – shape ecological systems. Over the last 30 years spatial ecology has developed as an integrative, multidisciplinary science that has improved our understanding of the ecological consequences of habitat fragmentation and loss. We argue that accelerating climate change – the effective manipulation of time by humans – has generated a current need to build an equivalent framework for temporal ecology. Climate change has at once pressed ecologists to understand and predict ecological dynamics in non-stationary environments, while also challenged fundamental assumptions of many concepts, models and approaches. However, similarities between space and time, especially related issues of scaling, provide an outline for improving ecological models and forecasting of temporal dynamics, while the unique attributes of time, particularly its emphasis on events and its singular direction, highlight where new approaches are needed. We emphasise how a renewed, interdisciplinary focus on time would coalesce related concepts, help develop new theories and methods and guide further data collection. The next challenge will be to unite predictive frameworks from spatial and temporal ecology to build robust forecasts of when and where environmental change will pose the largest threats to species and ecosystems, as well as identifying the best opportunities for conservation.

**Keywords**

Autocorrelation, climate change, ecological forecasting, events, non-stationarity, scaling, spatial ecology, temporal ecology.

*Ecology Letters* (2014)

Université de Sherbrooke

# Thank you for your attention!

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