PNAS LETTER

Reply to Ernst and Spaak: The LV-map accurately estimates species interactions even when functional responses are nonlinear

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In their Letter (1), Ernst and Spaak used a three-trophic-level system to argue that the LV-map cannot handle nonlinear functional responses because it merely fits local linear approximations, while the S-map is better suited to complex interactions. Here, we argue that the LV-map is, in fact, perfectly able to account for nonlinear functional responses, and we identify an error in their computation of coexistence metrics, specifically the sign of the interaction matrix in the Lotka–Volterra model formulation.

Ernst and Spaak applied the LV-map to a three-trophic-level system (2) with a Holling Type II functional response. As expected, the LV-map infers the local linearization of this response, leading to time-varying parameters. Notably, it correctly recovers the global picture of the system—a trophic chain (Fig. 1). Primary producers are consumed by herbivores, which are, in turn, preyed upon by secondary consumers, since lower-trophic-level species have positive effects on higher-trophic-level species, while the reverse effects are negative (Fig. 1 *C* and *D*). When computing

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The authors declare no competing interest.

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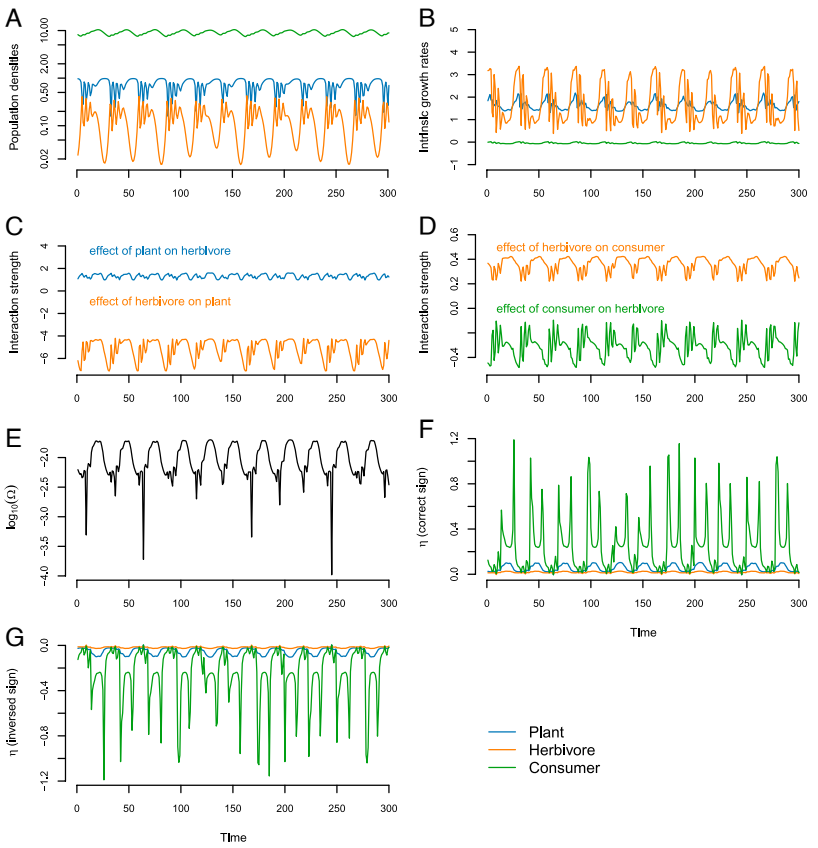

Fig. 1. LV-map applied to a three-trophic-level system with Holling Type II functional responses. (*A*) Population densities. (*B*) Inference of the intrinsic growth rates. (*C* and *D*) Inference of per-capita interaction strength. (*E*) Niche difference. (*F* and *G*) Values of resistance angles using positive sign and negative sign. Parameters used a_{ph} = 5, b_{ph} = 3, a_{hc} = 0.1, b_{hc} = 2, d_C = 0.01, and d_H = 0.4.

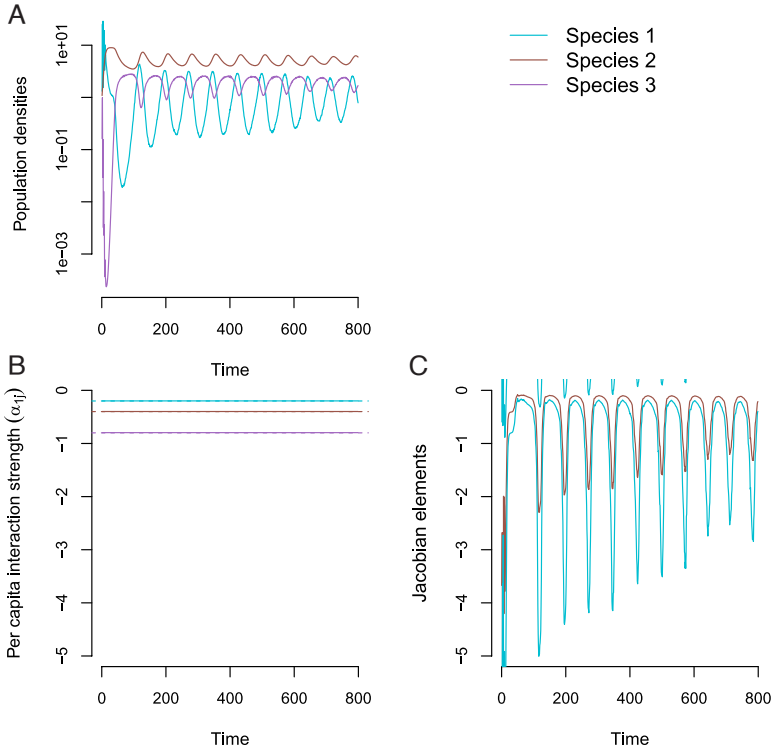

Fig. 2. Inference using S-map and LV-map on the cyclic population dynamics simulated from a Lotka–Volterra model of three competing species. (*A*) Population dynamics. Effect of all species on species 1 using LV-map (*B*) and using S-map (*C*). S-map produces fluctuating Jacobian estimates in a linear Lotka–Volterra system, while the LV-map recovers the true per-capita interaction strengths. Parameter used r = (3.8, 0.3, 2.4), and α = ([−0.2, −0.4, −0.8], [−0.001, −0.033, −0.067], [−0.2, −0.2, −0.6]).

coexistence conditions using the same parameter set and our code (figshare.10045976), we found opposite results compared to Ernst and Spaak: 98% of the time, all η values are positive, indicating coexistence of all three species (Fig. 1). This discrepancy stems from a crucial difference between their Lotka–Volterra formulation and ours. In their first equation (1), they place a negative sign in front of the per-capita interaction matrix, unlike the positive sign in our formulation [eq. 1, (3)]. While this does not affect LV-map inference, consistency between the LV-map output and the coexistence metric computation is required. We believe they inferred $\boldsymbol{\alpha}$, but used $-\boldsymbol{\alpha}$ to calculate their η_i, which inverts their findings: Their reported percentage of noncoexistence is actually a percentage of coexistence. The LV-map is therefore, as expected, robust to nonlinear functional responses.

Ernst and Spaak's description of the LV-map also requires clarification regarding the fundamental difference between the S-maps and LV-maps (3–5). Both methods rely on local linear regression, but the S-map's response variable is raw abundance, while the LV-map uses the per-capita growth rate. This distinction is crucial: The LV-map approach acknowledges the first principle of living organisms to reproduce, die, and interact on a per-capita basis (6–9)—a biological reality that S-map does not explicitly target. Consequently, the LV-map infers parameters with direct ecological meaning: intrinsic growth rates and per-capita interaction strengths. The S-map, by contrast, estimates the Jacobian matrix of the dynamical system (10, 11). Jacobian elements quantify the total effect of one species on another species' growth rate—inherently density-dependent and not equivalent to per-capita interaction strengths. To illustrate, we simulated a Lotka–Volterra model of three competing species: The LV-map recovers constant per-capita interaction strengths, while the S-map infers fluctuating Jacobian elements that should not be misinterpreted as fluctuating interaction strengths (Fig. 2).

In conclusion, the LV-map remains an accurate approach for inferring ecologically meaningful parameters—intrinsic growth rates and per-capita interaction strengths—from empirical time-series data of living organisms.

Data, Materials, and Software Availability. There are no data underlying this work.

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