Why study ecological interaction networks? Which questions?

Elisa Thébault











species



Chesapeake Bay food web Krause et al. (2003)





Rezende et al. 2007



Understand cascading effects in networks



Estes et al. (2011)

Model population dynamics

$$dN_i/dt = N_i \left(r_i + \sum_{j=1}^{n} \alpha_{ij} N_j \right)$$

Consequences on community functioning and stability



Consequences on community functioning and stability Understand cascading effects in networks



Cavalheiro et al. (2008)







Consequences on community functioning and stability Study the links between network structure and ecosystem responses to perturbations



Time

Questions

- What determines why there are links?
- What are the links between structure and function?
- What are the links between structure and stability?
- What is the structure of ecological networks? Are there structural generalities?
- How do networks change with environmental conditions?
- What is the role of interaction type?

Questions

- What determines why there are links? Today, example of species traits
- What are the links between structure and function?

Today, indirect interactions in networks + links with ecosystem function

• What are the links between structure and stability?

Tomorrow

- What is the structure of ecological networks? Are there structural generalities?
- How do networks change with environmental conditions?

Tomorrow + maybe Wednesday

• What is the role of interaction type?



Part I What determines the links between species? The role of traits

The example of body size in food webs



Trophic interactions and the ratio of body size between prey and predators



Brose et al. (2006)

Infering trophic interaction and food web structure from body size



Infering trophic interaction and food web structure from body size



Albouy et al. (2014)

Relations that depend on consumer traits and ecosystem types



Brose et al. 2019

Relations that depend on consumer traits and ecosystem types



Potapov et al. 2019

Different traits for different interaction types?



Different traits at different steps of a trophic interaction?



How many traits are required to predict an interaction?

	Ecology Letters				
	Ecology Letters, (2013)	doi: 10.1111/ele.12081			
LETTER	The dimensionality of ecological networks				

Few trait-axes (dimensions) are required to predict interactions between two species in a given network

Network	type	S	С	best1	best2	best3	bestAll
Puerto Rico, highland [†] (Dalsgaard et al. 2009)	bim	11 + 2	0.59	1 (BILc/BMc)	1 (BILc/BMc + any)	1 (BILc/BMc + any + any)	1 (9)
NZ landuse*	bim	15 + 16	0.17	0.44 (BWc)	0.79 (BWc + NDr)	0.91 (BWc + NDr + STIr)	0.98 (19)
Santa Genebra (Galetti & Pizo, 1996)	bim	29 + 33	0.14	0.40 (BIGc)	0.58 (BIGc + FSr)	0.65 (BiGc + FSr + BMc)	0.89 (11)
Villavicencio (Chacoff et al. 2012)	bim	41 + 80	0.18	0.35 (ORr)	0.46 (ORr + SLr)	0.56 (ORr + SLr + PWc)	0.90 (21)
Garraf (Bosch et al. 2009)	bim	19 + 165	0.26	0.62 (FBLr)	0.79 (FBLr + BLDr)	0.87 (FBLr + BLDr + POLr)	0.95 (12)
Ecuador LU-gradient (Tylianakis et al. 2007)	bia	29 + 9	0.18	0.58 (BLc)	0.75 (BLc + BLr)	0.75 (BLc + BLr + DPc)	0.75 (8)
NZ alpine grassland*	bia	38 + 31	0.085	0.34 (BMc)	0.74 (BMc + BMr)	0.75 (BMc + BMr + TMPc)	0.75 (6)
Ythan (Cohen et al. 2009)	fw	92	0.049	0.32 (BMc)	0.55 (BMc + BMr)	0.61 (BMc + BMr + HBc)	0.74 (12)
StMarks (Christian & Luczkovich, 1999)	fw	143	0.086	0.25 (BMc)	0.45 (BMc + MBr)	0.55 (BMr + MBr + HBc)	0.82 (12)
Caribbean reef (Optiz 1996)	fw	249	0.053	0.17 (BMr)	0.26 (BMr + BMc)	0.33 (BMr + BMc + MBr)	0.42 (12)
Kongsfjorden (Jacob et al. 2011)	fw	270	0.023	0.11 (MCr)	0.25 (HBr + BMc)	0.39 (MCr + BMc + MBr)	0.69 (12)
Loughhyne (Riede et al. 2010)	fw	349	0.042	0.15 (BMr)	0.24 (BMr + BMc)	0.33 (BMr + BMc + MBr)	0.47 (12)
Weddell (Jacob, 2005)	fw	488	0.067	0.20 (MBr)	0.30 (BMr + MBr)	0.40 (BMr + BMc + MBr)	0.61 (12)

*the data are available in Supporting Information.

†see Supporting Information for additional networks of the same type.

Trait identifiers: BIL, bill length; BM, body mass; BW, body width; ND, amount nectar; STI, flower type; BIG, bill gape; FS, fruit size; OR, orientation; SL, stamen length; PW, proboscis width; FBL, first bloom; BLD, bloom duration; POL, pollen volume per flower; BL, body length; DP, dates present; TMP, temperature envelope; HB, habitat; MB, mobility and MC, metabolic category.

Part I :What determines the links between species? The role of traits Some conclusions and perspectives

Importance of traits for understanding the structure of interaction networks: can we infer interactions between species?

Relative importance of given traits depending on interaction types, ecosystems, environmental conditions?

Relative importance of traits vs. abundance? Importance of evolutionary history?

Part II Network structure and ecosystem functioning

Diversity and ecosystem functioning



Tilman et al. (2006)

Hector et al. (2010)

Diversity and ecosystem functioning in ecological networks



Complementarity of the predation network

Poisot et al. 2013

Diversity of pollinators and functioning

PLOS BIOLOGY January 2006 | Volume 4 | Issue 1 | e1

Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities Colin Fontaine^{1,2*}, Isabelle Dajoz^{1,2}, Jacques Meriguet^{1,2}, Michel Loreau^{2,3}

Pollinators species	Mouthpart	Theoretical pollination		Plants species	Accessibility	
and groups	length (mm ± S.E.)		network	and groups	pollen	nectar
Sphaerophoria sp.	2.66 ± 0.35	a a	. All	M. officinalis	easy	easy
E. balteatus	$\textbf{2.3}\pm\textbf{0.20}$			E. cicutarium	easy	easy
E. tenax	5.47 ± 0.29	Syrphid-flie	Open flower	R. raphanistrum	easy	difficult
B. terrestris	9.02 ± 0.19	100	$\rightarrow \square$	M. guttatus	easy	difficult
B. hortorum	9.21 ± 1.02	- AF		M. sativa	difficult	difficult
B. lapidarius	8.10 ± 0.86	Bumble-bee	Tubular flower	L. corniculatus	difficult	difficult



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Diversity of pollinators and functioning

PLOS BIOLOGY January 2006 | Volume 4 | Issue 1 | e1 Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence

of Plant Communities Colin Fontaine^{1,2*}, Isabelle Dajoz^{1,2}, Jacques Meriguet^{1,2}, Michel Loreau^{2,3}





Diversity of pollinators and functioning other Frind,^{1,5} Carsten F. Dormann,^{2,3} Andrea Holzschull,^{1,4} and Teja Tscharntke¹

Bee diversity effects on pollination depend on functional complementarity and niche shifts

Ecology, 94(9), 2013, pp. 2042-2054





Diversity of pollinators and functioning other Frund,^{1,5} Carsten F. Dormann,^{2,3} Andrea Holzschull,^{1,4} and Teja Tscharntke¹

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Diversity of pollinators and ecosystem

services

Proc. R. Soc. B (2008) 275, 2283-2291

Functional group diversity of bee pollinators increases crop yield

Patrick Hoehn^{1,*}, Teja Tscharntke¹, Jason M. Tylianakis² and Ingolf Steffan-Dewenter³





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Table 4. Bee species richness and functional guild diversity in relation to the residuals of seed set after correlation with bee abundance. (Italic numbers indicate significant effects.)

	r^2	$F_{1,10}$	Þ
model 1			
bee species richness	0.32	6.08	0.033
functional guild diversity	0.15	2.87	0.121
model 2			
functional guild diversity	0.45	8.47	0.015
bee species richness	0.02	0.47	0.507

Ecology Letters, (2013)

doi: 10.1111/ele.12170

Diversity of pollinators and ecosystem against climate change

services (stability)

lgnasi Bartomeus, ^{1,2}* Mia G. Park,³ Jason Gibbs, ^{3,4} Bryan N. Danforth,³ Alan N. Lakso⁵ and Rachael Winfree^{1,6}

Insurance hypothesis

Species diversity decreases the variability of ecosystem properties through asynchronous response of species to environmental fluctuations





Yachi & Loreau (1999)

Time

Ecology Letters, (2013)

Diversity of pollinators and ecosystem Biodiversity ensures plant-pollinator phenological synchrony against climate change Ignasi Bartomeus, 1,2* Mia G. services (stability)

Park,³ Jason Gibbs,^{3,4} Bryan N Danforth,³ Alan N. Lakso⁵ and Rachael Winfree^{1,6}





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The structure of host-parasitoid networks and functioning

Complementarity and redundancy of interactions enhance attack rates and spatial stability in host-parasitoid food webs

Guadalupe Peralta,^{1,6} Carol M. Frost,¹ Tatyana A. Rand,² Raphael K. Didham,^{3,4} and Jason M. Tylianakis^{1,5}

Peralta et al. 2014



Part II: Network structure and ecosystem functioning Some conclusions and perspectives

- Network structure allows to describe complementarity and redundancy among species -> direct links with the study of ecosystem functions and stability
- Studies often focus on one or two trophic levels: need a food web perspective?
 Species richness and food-web structure jointly drive community


Part III Cascading effects in networks Network structure and indirect interactions

Understanding indirect effects: a central issue in ecological networks



Understanding direct and indirect effects: studies on network motifs





Understanding direct and indirect effects: studies on network motifs



- r = intrinsic growth rate of R
- K = carrying capacity of R
- a_{NR} and a_{PN} are the attack rates
- e_{NR} and e_{PN} are the conversion efficiencies
- d_N and d_P are the mortality rates

$$\frac{dP}{dt} = P(-d_P + e_{PN}a_{PN}N)$$

$$\frac{dN}{dt} = N(e_{NR}a_{NR}R - d_N - a_{PN}P)$$

$$\frac{dR}{dt} = R(r(1 - R/K) - a_{NR}N)$$



• If there is an equilibrium with all species present, then:

$$P^* = \frac{1}{a_{PN}} \left(e_{NR} a_{NR} R^* - d_N \right)$$

$$N^* = \frac{d_P}{e_{PN}a_{PN}}$$

$$R^* = K\left(1 - \frac{a_{NR}}{r}N^*\right)$$

• If there is an equilibrium with all species present, then:



• With 4 species in the food chain:

$$P_2^* = \frac{1}{a_{P2P}} (e_{PN} a_{PN} N^* - d_P)$$
$$P^* = \frac{d_{P2}}{e_{P2P} a_{P2P}}$$
$$N^* = \frac{1}{a_{NR}} \left(1 - \frac{R^*}{K}\right)$$
$$R^* = \frac{d_N + a_{PN} P^*}{e_{NR} a_{NR}}$$









Wootton & Power 1993



Ware & Thomson Science 2005

Another example of food chain model

Consumer functional response is ratio-dependent



• If there is an equilibrium with all species present, then:



Effects can differ from predictions



Table 1 Qualitative effects of nutrient enrichment as predicted by two linear food-chain models and corresponding experimental results in mesocosms

	Model predictions		Experimental results	
	Prey dependence	Ratio dependence	Without fish	With fish
Carnivores	+	+	_	§
Herbivores	0	+	ns	ns
Autotrophs	+	+	ns	ns
Phosphorus	0	+	ns	+

Qualitative effects are indicated by their sign: +, 0 and – denote a positive effect, no effect and a negative effect, respectively, of nutrient enrichment on density. Experimental results: + and – denote a significant positive effect and a significant negative effect, respectively ($P \le 0.05$); brackets, marginally significant effect (0.05 < $P \le 0.10$); ns, nonsignificant effect (P > 0.10); §, no test possible because the sum of invertebrate carnivores density and fish biomass is senseless.

Hulot et al. Nature 2000

Need to consider food web structure



Simplified pelagic food web

(from Carpenter et Kitchell, 1993, *The trophic cascade in lakes,* Cambridge University Press).







Hulot et al. Nature 2000







Hulot et al. Nature 2000



Wollrab et al. 2012



Wollrab et al. 2012



Wollrab et al. 2012



McCann & Rooney 2009





Primary production (t WW km-2 year-1)

Understanding direct and indirect effects: studies on network motifs



Understanding direct and indirect effects apparent competition



Morris et al. 2004

Understanding direct and indirect effects apparent competition



Morris et al. 2004

Important applications for management

ELSEVIER	Available online at www.sciencedirect.com	Agriculture Ecosystems & Environment			
Enhancing parasitism of wheat aphids through apparent			Ecology Lett	ters, (2008) 11 : 690–700	doi: 10.1111/j.1461-0248.2008.01184.x
	Alain Langer ¹ , Thierry Hance*	LETTER	Appare of high	nt competition can ly specific biocontro	compromise the safety I agents
	+ +		Carvalhe	iro et al. (2008)	
	+ + Ecology Lette	RS	ELSEVIER	GfÖ Ecological Society of Germany, Austria and Switzerland Basic and Applied Ecology 63 (2022) 36–	48 Basic and Applied Ecology
	Ecology Letters, (2014) 17: 1389–1399	doi: 10.1111/ele.12342	RESEARCH PAPER		
LETTER The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness		Co-flowering plants support diverse pollinator populations and facilitate pollinator visitation to sweet cherry crops			
		Amy-Marie Gilpin ^a ,*, Corey O'Brien ^a , Conrad Kobel ^b , Laura E. Brettell ^{a,c} , James M. Cook ^a , Sally A. Power ^a			

Carvalheiro et al. (2014)

Indirect effect of species *j* on species *i*:

The Structure of an Aphid-Parasitoid Community

C. B. Muller; I. C. T. Adriaanse; R. Belshaw; H. C. J. Godfray

The Journal of Animal Ecology, Vol. 68, No. 2 (Mar., 1999), 346-370.







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Indirect effect of species *j* on species *i*:



Fraction of predators of species *i* that belong to predator species *k*



C. B. Muller; I. C. T. Adriaanse; R. Belshaw; H. C. J. Godfray

The Journal of Animal Ecology, Vol. 68, No. 2 (Mar., 1999), 346-370.



Predators or parasitoids

Prey



 α_{jk}

 α_{mk}

Indirect effect of species *j* on species *i*:

 $d_{ij} = \sum_{k}$

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Fraction of predators of species *i* that belong to predator species *k*

Fraction of predator species k attacking species j





Indirect effect of species *j* on species *i*:

$$d_{ij} = \sum_{k} \left(\frac{\alpha_{ik}}{\sum_{l} \alpha_{il}} \times \frac{\alpha_{jk}}{\sum_{m} \alpha_{mk}} \right)$$

 $d_{ji} \neq d_{ij}$

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Prey





Primary parasitoids (scale: aphids × 58

Competition or facilitation in plant-pollinator networks?

Complex indirect interactions among plants and among pollinators, importance of the balance between mutualism and competition

Bastolla et al. (2009) Valdovinos et al. (2016) 80 В 2016 2017 60 Α Seeds per flower Pollinators 40 Facilitation Competition 20 Fitness Plants Species B Species A High 0 High acting target Target degree Target degree 0.8 1.0 0.2 0.4 0.6 degree degree Target degree

Bergamo et al. 2021

Predicting cascading effects in complex ecological networks?



Need for a dynamical perspective and accounting for long indirect pathways



Pires et al. (2020)

Predicting cascading effects in food webs? How different species affect the effect of one predator on one prey



Yodzis 2000

Predicting cascading effects in food webs? How different species affect the effect of one predator on one prey



$$\frac{dB_i}{dt} = r_i B_i \left(l - \frac{B_i}{K_i} \right) - \sum_k F_{ik} B_k - H_i \equiv g_i$$
$$\frac{dB_i}{dt} = \left(-T_i + \sum_k (1 - \delta_k) F_{ki} \right) B_i - \sum_k F_{ik} B_k - I_i B_i^2 - H_i \equiv g_i.$$
Jacobian matrix : $A_{ij} = \left[\frac{\partial g_i}{\partial B_j} \right]_e$

The long-term change in the biomass of species i in response to a change in seal rate of cull is given by

$$R(i, s) \equiv \frac{dB_i^{\mathsf{e}}}{dH_s} = (\mathbf{A}^{-1})_{is} \tag{7}$$
Predicting cascading effects in food webs? How different species affect the effect of one predator on one prey



$$\frac{dB_i}{dt} = r_i B_i \left(l - \frac{B_i}{K_i} \right) - \sum_k F_{ik} B_k - H_i \equiv g_i$$
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The long-term change in the biomass of species i in response to a change in seal rate of cull is given by

$$R(i, s) \equiv \frac{dB_i^{\mathsf{e}}}{dH_s} = (\mathbf{A}^{-1})_{is} \tag{7}$$

$$R(i, s; o) \equiv \left[\frac{dB_i^{e}}{dH_s}\right]_{dB_o^{e}=0} = (\mathbf{A}^{-1})_{is} - \frac{(\mathbf{A}^{-1})_{io}(\mathbf{A}^{-1})_{os}}{(\mathbf{A}^{-1})_{oo}}$$

Yodzis 2000

Predicting cascading effects in food webs? How different species affect the effect of one predator on one prey



$$\frac{dB_i}{dt} = r_i B_i \left(l - \frac{B_i}{K_i} \right) - \sum_k F_{ik} B_k - H_i \equiv g_i$$
$$\frac{dB_i}{dt} = \left(-T_i + \sum_k (1 - \delta_k) F_{ki} \right) B_i - \sum_k F_{ik} B_k - I_i B_i^2 - H_i \equiv g_i$$
$$\text{Jacobian matrix}: \quad A_{ij} = \left[\frac{\partial g_i}{\partial B_j} \right]_e$$

Influence of a species o on the response of species i to a cull of seals s:

$$I(i, s; o) \equiv \frac{R(i, s; o) - R(i, s)}{R(i, s)}$$
$$= \frac{(\mathbf{A}^{-1})_{io}(\mathbf{A}^{-1})_{os}}{(\mathbf{A}^{-1})_{oo}(\mathbf{A}^{-1})_{is}}.$$

Yodzis 2000

« Diffuse effects in food webs »





« Diffuse effects in food webs »







Montoya et al. 2009

TABLE 3. Sign structure of the Jacobian matrix C and of its inverse C^{-1} .

	Same sign		Different sign	
Food web	%	log mean $ c_{ij} $	%	$\log \text{mean } c_{ij} $
Ythan	54.4	-1.41***	45.6	-1.59***
Broadstone	54	0.16***	46	-0.28***
Soil 1	63.1	0.38	36.9	0.17
Soil 2	53.8	0.12***	46.2	0.46***
Soil 3	63.2	0.45***	36.8	0.3***
Soil 4	57.9	0.44	42.1	0.46
Soil 5	66.7	0.78***	33.3	0.55***
Soil 6	77.8	0.85***	22.2	-0.20^{***}
Soil 7	57.5	0.13***	42.5	-0.04^{***}
Mean	60.93		39.07	

Bioenergetic model of Yodzis and Innes (1992)

$$\frac{dC}{dt} = C \left(-T + (1 - \delta)J_{\max} \frac{R^n}{R^n + R_0^n} \right)$$
$$\frac{dR}{dt} = rR \left(1 - \frac{R}{K}\right) - C \frac{J_{\max}}{f_e} \frac{R^n}{R^n + R_0^n}$$

T = mass-specific respiration rate of the population $T = a_T m_C^{-0.25}$ (respiration per unit biomass)



Bioenergetic model of Yodzis and Innes (1992)

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T = mass-specific respiration rate of the population (respiration per unit biomass)

$$T = a_T m_C^{-0.25}$$

J = mass-specific ingestion rate of the population

$$(1 - \delta)J_{\text{max}} = f_J a_J m_C^{-0.25}$$



Bioenergetic model of Yodzis and Innes (1992)

$$\frac{dC}{dt} = C \left(-T + (1 - \delta)J_{\max} \frac{R^n}{R^n + R_0^n} \right)$$
$$\frac{dR}{dt} = rR \left(1 - \frac{R}{K}\right) - C \frac{J_{\max}}{f_e} \frac{R^n}{R^n + R_0^n}$$

T = mass-specific respiration rate of the population (respiration per unit biomass)

J = mass-specific ingestion rate of the population r = intrinsic production-biomass ratio

$$T = a_T m_C^{-0.25}$$

(1-\delta) $J_{\text{max}} = f_J a_J m_C^{-0.25}$
 $r = f_r a_r m_R^{-0.25}$



Predicting cascading effects in complex food webs?



Predicting cascading effects in complex food webs?





Iles & Novak 2016

Part III: Cascading effects in networks Network structure and indirect interactions Some conclusions and perspectives

Importance of indirect interactions: network structure matters for understanding cascading effects in ecological communities

> Can we predict consequences of perturbations on ecological networks?

Which network structures limit the spread of cascading effects? See the course tomorrow on structure and stability