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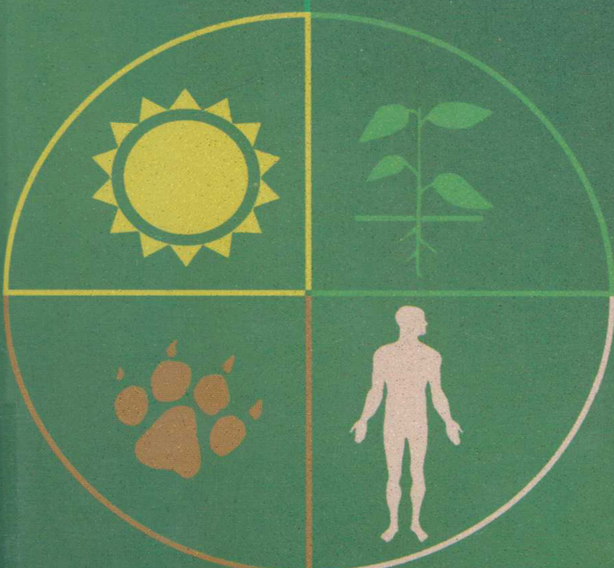
# Ecological Networks

# 生态网络

Guy Woodward



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原版引进

科学出版社

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# 生 态 网 络

Edited by

**Guy Woodward**

School of Biological and Chemical Sciences,

Queen Mary University of London,

London E1 4NS, UK

科 学 出 版 社

北 京

**图字：01-2011-4493**

This is an annotated version of
**Ecological Networks.**
Edited by Guy Woodward.



ISBN：978-0-12-381363-3.



**图书在版编目(CIP)数据**

生态网络＝Ecological Networks：英文／(英) 伍德沃德 (Woodward, G.) 主编. —北京：科学出版社，2012
(生态前沿系列)
ISBN 978-7-03-034143-3
Ⅰ. ①生… Ⅱ. ①伍… Ⅲ. ①生态学—研究—英文 Ⅳ. ①Q14
中国版本图书馆 CIP 数据核字 (2012) 第 080765 号

责任编辑：孙红梅／责任印制：钱玉芬
封面设计：耕者设计工作室

科学出版社 出版
北京东黄城根北街 16 号
邮政编码：100717
http://www.sciencep.com
双青印刷厂 印刷
科学出版社发行 各地新华书店经销
*
2012 年 5 月第 一 版 开本：B5 (720×1000)
2012 年 5 月第一次印刷 印张：29
字数：585 000
**定价：135.00 元**
(如有印装质量问题，我社负责调换)

# 导 读

生态学（Ecology）一词较早出现于德文——Ökologie，是1865年由勒特（Reiter）将希腊字Oikos（居所）和Logs（研究）合并而成（Frodin 2001）。德国动物学家和哲学家恩斯特·海克尔（Ernst Haeckel）于1866年首先定义了生态学的概念，现多表述为：生态学是研究生物与其环境之间的相互关系及其作用机制的科学。除了关注生物个体与环境间的关系外，传统生态学研究者进行最多的是在生物种群和群落水平上的研究，得出了一些结论：认为在一个群落内任何物种都与其他物种存在着相互依赖和相互制约的关系，如生物链中捕食者和被捕食者间的数量保持相对稳定的关系、彼此间的竞争和互利共生关系、能量的流动转换定律等，这些都是生态学的经典研究内容，有些结论被认为不可颠覆。然而，后来其中的许多观点和结论受到了挑战。特别是自20世纪50年代以来，由于数学、物理、化学及工程技术等先进的自然科学研究成果被生态学广泛采用，并伴随着精密仪器和计算机技术在生态学中的应用，使得生态学研究从粗放走向精准，从定量走向定性，特别是对复杂的生态现象可以进行定量的准确分析描述，使得生态学研究者可以从整体框架出发，分析其结构组分及功能的变化动态及其环境控制机制，阐述生物种群、群落的层次性和系统性，直到定量分析自然的复合系统——生态网络。

其实，有关生态网络的概念由来已久，很早就有了萌芽，只不过由于条件的限制没有得到很好的研究和重视。早在1859年，达尔文（Charles Darwin）撰写的《物种起源》一书中就描述了一个“纷繁的河岸”：那儿林木交错、虫鸟欢叫、蚯蚓蠕动，这是何等交互依存的复杂景象！而后，早期著名生态学家Forbes（1887）也提出：动植物相互联系地共存于一个有机复杂体系中，而他们的相互作用又影响着这个复杂体系的状态，这或许是生态网络概念的萌芽。然而，也许正因其复杂性，使得生态网络作为生态学的一个学科分枝，发展得相当缓慢，可以说在很长的一个历史阶段中都处在一个概念提出和定性描述阶段，缺乏系统的定量分析研究。直到最近，生态网络的研究工作才重新得到关注，特别是在食物网、寄主-寄生物网、互利共生网络三个方面受到了广泛重视，并已经取得了颇丰的阶段性研究成果（e.g. Woodward *et al.*, 2005a，Pascual and Dunne，2006；Bascompte and Jordano，2007；Ings *et al.*, 2009；Olesen *et al.*, 2010）。如，最近的拓扑型分析表明，是生态网络的复杂性构型和交互强度的分布控制了其网络的结构和稳定性，而不仅是它变异幅度的多寡。生态网络研究主要是研究

物种间复杂结构、交互作用，探索时空变化规律，阐明复杂系统内部结构，对比分析不同生态系统的特异性，进而探讨保持自然系统的可持续性方式和策略，主要研究内容包括“传统”食物网、互利共生生态网、宿主和寄生物网三个部分等，重点比较不同类型间的差异及其潜在环境控制机制，明确生态网络的结构布局及其层次，探索在自然环境或人类干扰条件下其内在的交互作用在进化中所扮演的重要角色，以试图为遏制生态环境退化、物种入侵和减轻气候变化的负面影响提供理论指导和技术支持（Ings *et al.*，2009）。

本卷第一篇，作者着眼于动态分析而非静态分析，以英格兰的 Broadstone 溪流网络和格陵兰的 Zackenberg 的传粉网络为例，深入分析系统内部结构、时空异质性及其层次特性。特别是针对生态网络中物种间的联系大约缺失了 80%，这为什么不像我们期望的那样应该是彼此间相互密切联系的呢？为了回答这个问题，Olesen 及其合作者在分析研究的基础上，指出这些未被察觉到的关联也许是被“丢失”了或被“禁止”了，而存在物候上的或生理代谢上的不匹配可能是其原因之一。气候变化已经发生而且继续发生，与生物个体、种群乃至生态系统的相互作用研究甚多，但针对气候变化与生态网络相互作用的复杂分析甚少。本卷的第二篇则讨论了这方面的研究结果。作者首先提出针对研究气候变化和生态网络相互关系的若干研究方法；其后论述了如何正确评估气候变化组分的影响，探讨了从个体、群落等较低层次得到的一般规律能否解释生态网络上的复杂规律？接着论述了这些气候组分是如何联合或交互地影响到生态网络的结构和稳定性的。第三章针对传统营养尺度转换研究的不足，在分析复杂参数尺度独立性的基础上，作者 Riede 等收集到了 65 个不同类型的食物网数据，提出了 19 个食物网拓扑参数，并发现他们与多样性和复杂性等有明显的幂律尺度转换关系。最后探讨了不同生态系统类型组成对分析结果的可能影响。第四章的内容是作者 McLaughlin 等在收集了一个位于爱尔兰科克西南部的林下食物网的样本及其数据的基础上，分析研究了物种个体大小与多度、捕食者-猎物关系的稳定性、动态变化规律，及其生态系统类型的影响。第五章的研究则是利用高度成熟的 20 个标准化食物网，论述了生态网络的结构、动态及其决定因素是如何随一个环境梯度（pH 值梯度，5.0～8.4）变化的？进而评价外部环境和内部生物因素对网络的结构及其稳定性的影响。作者所利用的资料数据和环境梯度都是弥足珍贵的。本卷的最后一章，作者在爱尔兰西南岸的海底设置 24 座笼罩，建立了一个易于操作的底栖海洋生态系统研究平台，通过实施这个较大规模的中型实验生态系统实验，评估剔除物种对网络结构整体性及其稳定性的影响，最后着重指出：

个体大小、数量多度、生物量多度在每个独立的营养水平上基本保持不变，进一步支持了生态位分化的理论；不管生态系统的多样性、稳定性及其生产力如何，异速生长关系和群落中物种个体大小及其结构在保持生态网络结构的可持续性方面都具有重要意义。读罢本章，能使我们感到：正如所了解的那样，尽管生态网络实验研究需要的时间长，难度大，复杂性高，感觉迷茫而无从下手，而此章可作为我们的典范之作。

所有这些，都从一个全新的视角，应用较新的分析手段帮助我们了解生态网络中各个节点间的关系、结构特性、稳定性及其时空变化的真实状态，读来大有裨益。然而，值得注意的是，那些成功建立起来的生态网络的稳定性是相对的，而受到外界的打扰是绝对的，就算那些建立在远离大陆的海岛上的实验研究区域也阻止不了与外界的源源不断的交流，如总有不可预测的珍稀物种的侵入和候鸟的偶然栖息。所以，生态网络实验研究的不可预见性在所难免。也许正因如此，国际上关于生态网络的研究正在迅速崛起，研究领域异常活跃，生态网络的复杂性也许正是其令人神往的穷究之处。

该书具有如下特性：一是注重与传统生态学的连续性。所研究的生态学参数如个体大小、物种多度等都是我们比较熟悉的，使人感到入门不难，可增强研究生态网络的信心。二是具有前沿性。自然系统的复杂性是目前有关生态科学研究的难点，本卷生态网络的研究实施者似乎找到了问题的突破口，如充分利用现有的成熟食物网的参数资料等，并取得了一些前沿性的研究结果。三是科学问题的急迫性。气候变化与生态网络的相互作用正是当前我们需要亟待澄清的问题。气候变化对生物个体及其生理生态机制影响的研究比较透彻，在种群、群落、生态系统乃至景观水平上的研究也都收获颇丰，然而，气候变化是如何影响生态网络的结构和稳定性的？在未来气候变化情景下生态网络的可持续性如何？这些都是我们为了应对气候变化的负面影响，保护地球上的生命维持系统而迫切需要解决的。四是实用性。本书所提供的实验设计、研究平台、概念参数和数据分析方法等都简明可行，易于操作，便于直接获取，为深入研究生态网络提供了便利之门。五是文献的新颖性。本卷的作者都是目前活跃在生态学研究领域的重要研究者，他们所报道的都是最近几年的研究成果，具有较强的参考价值。

诚然，生态网络的研究和我们所熟知的种群生态学、生态系统生态学、景观生态学、全球变化生态学等较大层次上的研究在内容上有所重叠和交叉，但前者更强调复杂系统中各要素的相互作用及其对系统稳定性的影响、动态变化

规律，研究的广度、难度和维度更大更深，更易使人“眼花缭乱”。然而，正因如此，未开垦的“五彩缤纷”处女之地也许更引人入胜，吸引有志者耕耘不辍，在超越中获取大自然赐予我们的瑰宝——生态网络的真谛。期望酌读此卷如它山之石、点睛之笔，能在探索生态学奥秘的知识海洋中有所启迪、有所收获。

许振柱　研究员
E-mail：xuzz@ibcas. ac. cn
中国科学院植物研究所

# 前　　言

## 生态网络：不断变化的世界中复杂系统的简单规律？

本卷《生态学研究进展》的主题是有关生态网络的研究——即发生在个体及至更高层次的生物组织，如种群或个体体型等级中，由对抗或共生作用所形成的物种关系网络。1859 年，达尔文在《物种起源》一书中首先使用“喧闹纷繁的河岸”来比喻物种间复杂相互作用的关系网络。20 年后，Camerano 于 1880 年描述了首个被认可的表示食物网的球棒模式。那时，许多著名的先锋生态学家，如 Elton（1927）、Lindeman（1942）、MacArthur（1955）和 Hutchinson（1959）等，也都关注这些网络系统的研究，其中，有的首次提出自然系统的复杂性可能赋予了其稳定性，并指出物种个体大小在构建群落和决定相互作用强度的过程中扮演了重要角色。然而，这些早期有关系统复杂性和稳定性相联系的思想受到了著名模型研究者 May（1972，1973）及其他很多人的质疑，他们的数学模型模拟表明，系统的复杂性削弱了其稳定性。这样就引出了一个长期悬而未决的问题，即维持自然界中复杂食物网的潜在机制到底是什么呢？

自 20 世纪 90 年代以来，人们构建了一批新的食物网，从中获得了大量可供分析的样本，明确了其所包含的分类特征，并结合新的数学模型进行模拟分析，共同解释复杂系统是如何维持稳定性的——如果物种间的相互关系很微弱的话？（如 McCann，Hastings and Huxel，1998）。那时起，很多研究都从实验和理论两个角度表明了消费者的体型大小及其所利用的资源是决定物种间相互作用强度、网络结构及其稳定性的关键因素（如 Berlow *et al.*，2009；Emmerson and Raffaelli，2004）。近二十年来，从开展新的相关研究计划及成倍增加的出版文献数量等方面都可以看出，有关生态网络的研究取得了许多开创性成果（Ings *et al.*，2009）。如今不同类型的高质量数据足以让生态学家们能够进行有意义的整合分析、在大范围系统内搜索涉及网络结构和动态的宏观生态学模式。然而，直到最近，正如本卷作者 Riede 及其合作者所强调的那样，由于收集数据的不足或不一致，阻碍了有关两个区域的研究进展。另外，最近通过从共生网络的角度研究植物的开花行为（如植物-传粉者网络）、借鉴社会科学网络研究中有关杂交的思路，已经补充完善了传统食物网和宿主-寄生者网络的研究。这些研究成果都包含在 Olesen 等人的全面评述和综合性论文中。因此，我们现在可以编写和逐步概括出网络结构及其动态的一般特征，

并开始建立预见性框架来预测它们对自然和人为干扰的可能响应。近年来，一个反复出现并贯穿本卷多处的主题就反映了很多早期生态学家（尤其是 Elton 和 Hutchinson）提出的思想：个体大小具有关键作用（Cohen *et al.*，2003），而且与其相关的因素（如基础代谢速率）的影响能从食物网中分离出来。

本卷的首篇是由 Olesen 等人（2010）概述了关于网络研究的八个关键领域的现状和前景，包括对网络结构的深层思考及其随着时空变化的特征描述。Woodward 等（2010）撰写的第二篇文章提出了一个基于第一性原理的主要涉及代谢制约和生态化学计量学方面的理论新框架，为进一步阐明网络水平上对气候变化的响应机制提供了可能的研究途径。接下来的篇章主要是依据从许多不同生态系统，包括海洋、淡水和陆地食物网等取得的详尽实验数据而展开论述。其中第一篇报道了 Riede 等人（2010）利用一个高质量的新数据库对网络属性进行整合分析的结果，为网络尺度与一系列食物网参数之间存在的幂律关系提供了有力证据。McLaughlin 等（2010）在深入研究一个较成熟的陆地地上和地下食物网的基础上，探讨了网络的属性及其尺度与结构的关系。本卷倒数第二篇文章由 Layer 等人（2010）撰写，是关于宏观生态学和模型方面的研究，内容涉及了 20 条溪流的食物网，涵盖了一个变化较大的 pH 值梯度，是首批尝试阐明环境胁迫因子如何影响并改变网络结构和稳定性的研究之一。O'Gorman 和 Emmerson（2010）撰写了本卷最后一篇文章，他们利用一个海洋底栖食物网仔细分析个体大小的作用，并从一个可重复的野外实验结果中概括了高度成熟的生态网络的特征。

总之，本卷的六篇文章涵盖了甚为广泛的生态系统类型（包括海洋、淡水和陆地生态系统）、生态网络类型（食物网、共生网络和宿主—寄生者网络）等，也体现了理论和实验方法的结合。虽然个体大小的作用在每章中都被提及，但这并非意味着仅仅强调这一点，尽管它确实是一个有用的能在网络中反映许多相关生物学变量的关键环节。我们知道，有关残差分析方法可为我们提供更多极高价值的与其他许多重要的生态学特性和现象（如特有物种的特性、适应性行为和系统发育制约等）相关的信息；否则，这些重要信息将被淹没。在很多情况下，尤其是水生生态系统，可把个体大小作为一把相对简单的标尺来帮助我们了解乃至预测这些复杂生态网络的结构和动态，及其对未来环境变化的响应。这项工作看似相当艰巨，但研究前景令人兴奋，而此卷的编写能使我们更加接近这个目标。

Guy Woodward

（许振柱　译）

# 参考文献


Berlow, E. A. , Dunne, J. A. , Martinez, N. D. , Starke, P. B. , Williams, R. J. , and Brose, U. (2009) . Simple prediction of interaction strengths in complex food webs. *Proc. Natl. Acad. Sci. USA* 106, 187-191.

Camerano, L. (1880) . Dell' equilibrio dei viventi mercéla reciproca distruzione. *Atti della Reale Accademia delle Scienze di Torino* 15, 393-414.

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

Darwin, C. (1859) . On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.

Elton, C. S. (1927) . *Animal Ecology*. Sedgewick and Jackson, London.

Emmerson, M. , and Raffaelli, D. (2004) . Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* 73, 399-409.

Hutchinson, G. E. (1959) . Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* 93, 145-159.

Ings, T. C. , Montoya, J. M. , Bascompte, J. , Bluthgen, N. , Brown, L. , Dormann, C. F. , Edwards, F. , Figueroa, D. , Jacob, U. , Jones, J. I. , Lauridsen, R. B. , Ledger, M. E. *et al*. (2009) . Ecological networks—Beyond food webs. *J. Anim. Ecol.* 78, 253-269.

Lindeman, R. L. (1942) . The trophic-dynamic aspect of ecology. *Ecology* 23, 399-418.

Layer, K. , Riede, J. O. , Hildrew, A. G. , and Woodward, G. (2010) . Food web structure and stability in 20 streams across a wide pH gradient. *Adv. Ecol. Res.* 42, 267-301.

MacArthur, R. (1955) . Fluctuations of animal populations and a measure of community stability. *Ecology* 36, 533-536.

May, R. M. (1972) . Will a large complex system be stable? *Nature* 238, 413-414.

May, R. M. (1973) . Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.

McCann, K. , Hastings, A. , and Huxel, G. R. (1998) . Weak trophic interactions and the balance of nature. *Nature* 395, 794-798.

McLaughlin, O. B. , Jonsson, T. , and Emmerson, M. C. (2010) . Temporal variability in predator-prey relationships of a forest floor food web. *Adv. Ecol. Res.* 42, 173-266.

O'Gorman, E. J. , and Emmerson, M. C. (2010) . Manipulating interaction strengths and the consequences for trivariate patterns in a marine food web. *Adv. Ecol. Res.* 42, 303-421.

Olesen, J. M. , Dupont, Y. L. , O'Gorman, E. J. , Ings, T. C. , Layer, K. , Melián, C. J. , *et al*. (2010) . From Broadstone to Zackenberg: Space, time and hierarchies in ecological networks. *Adv. Ecol. Res.* 42, 1-70.

Riede, J. O., Rall, B. C., Banasek-Richter, C., Navarrete, S. A., Wieters, E. A., and Brose, U. (2010). Scaling of food-web properties with diversity and complexity across ecosystems. *Adv. Ecol. Res.* 42, 141-172.

Woodward, G., Benstead, J. P., Beveridge, O. S., Blanchard, J., Brey, T., Brown, L. E., *et al.* (2010). Ecological networks in a changing climate. *Adv. Ecol. Res.* 42, 71-139.

# Contributors to Volume 42

**CAROLIN BANASEK-RICHTER,** *Environmental Research Institute, University College Cork, Lee Road, Cork, Ireland and School of Biology, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland.*

**JONATHAN P. BENSTEAD,** *Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, USA.*

**OLIVER S. BEVERIDGE,** *Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield, S10 2TN, United Kingdom. and School of Biological and Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, United Kingdom.*

**JULIA BLANCHARD,** *Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 OHT, United Kingdom.*

**THOMAS BREY,** *Alfred Wegener Institute for Polar and Marine Research, PO 120161, 27515, Bremerhaven, Germany.*

**ULRICH BROSE,** *Systemic Conservation Biology Group, J.F. Blumenbach Institute of Zoology and Anthropology, Georg-August-University Goettingen, Germany.*

**LEE E. BROWN,** *School of Geography, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, United Kingdom.*

**WYATT F. CROSS,** *Department of Ecology, Montana State University, Bozeman, MT 59717, USA.*

**YOKO L. DUPONT,** *Department of Biological Sciences, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark.*

**MARK C. EMMERSON,** *Environmental Research Institute, University College Cork, Lee Road, Cork, Ireland; School of Biology, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland; Department of Zoology, Ecology and Plant Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland and Queens University Belfast, School of Biological Sciences, Medical Biology Centre, 97 Lisburn Road, Belfast, BT9 7BL, Northern Ireland.*

**NIKOLAI FRIBERG,** *National Environmental Research Institute, Department of Freshwater Ecology, Aarhus University, Vejlsøvej 25, DK-8600 Silkeborg, Denmark.*

**ALAN G. HILDREW,** *School of Biological & Chemical Sciences, QueenMary University of London, London, E1 4NS, United Kingdom.*

**THOMAS C. INGS,** *School of Biological & Chemical Sciences, Queen Mary University of London, London, E1 4NS, United Kingdom.*

**UTE JACOB,** *Institute for Hydrobiology and Fisheries Science, University of Hamburg, Grosse Elbstrasse 133, D-22767 Hamburg, Germany.*

**SIMON JENNINGS,** *Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 OHT, United Kingdom.*

**TOMAS JONSSON,** *Ecological Modelling Group, Research Centre for Systems Biology, University of Skövde, P.O. Box 408, SE-541 28 Skövde, Sweden.*

**KATRIN LAYER,** *School of Biological & Chemical Sciences, Queen Mary University of London, London, E1 4NS, United Kingdom.*

**MARK E. LEDGER,** *School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom.*

**ÓRLA B. MCLAUGHLIN,** *Environmental Research Institute, University College Cork, Lee Road, Cork, Ireland and School of Biology, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland.*

**CARLOS J. MELIÁN,** *National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101.*

**ALEXANDER M. MILNER,** *School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom.*

**JOSE M. MONTOYA,** *I Institute of Marine Sciences, Consejo Superior de Investigaciones Científicas, Passeig Maritim Barceloneta 37–49, 08003, Barcelona, Spain.*

**SERGIO A. NAVARRETE,** *Estación Costera de Investigaciones Marinas & Center for Advanced Studies in Ecology & Biodiversity, Depto. de Ecología Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.*

**EOIN O'GORMAN,** *School of Biology and Environmental Science, Science Centre West, University College Dublin, Belfield, Dublin 4, Ireland.*

**JENS M. OLESEN,** *Department of Biological Sciences, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark.*

**OWEN L. PETCHEY,** *Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield, S10 2TN, United Kingdom.*

**DORIS E. PICHLER,** *School of Biological & Chemical Sciences, Queen Mary University of London, London, E1 4NS, United Kingdom.*

**BJÖRN C. RALL,** *Systemic Conservation Biology Group, J.F. Blumenbach Institute of Zoology and Anthropology, Georg-August-University Goettingen, Germany.*

**DANIEL C. REUMAN,** *Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire, SL5 7PY, United Kingdom.*

**JENS O. RIEDE,** *Systemic Conservation Biology Group, J.F. Blumenbach Institute of Zoology and Anthropology, Georg-August-University Goettingen, Germany.*

**CLAUS RASMUSSEN,** *Department of Biological Sciences, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark.*

**MURRAY S.A. THOMPSON,** *School of Biological & Chemical Sciences, QueenMary University of London, London, E1 4NS, United Kingdom and Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.*

**KRISTIAN TRØJELSGAARD,** *Department of Biological Sciences, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark.*

**FRANK J. F. VAN VEEN,** *School of Bioscience, The University of Exeter, Exeter, Devon, EX4 4SBUnited Kingdom.*

**EVIE A. WIETERS,** *Estación Costera de Investigaciones Marinas & Center for Advanced Studies in Ecology & Biodiversity, Depto. de Ecología Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.*

**GUY WOODWARD,** *School of Biological & Chemical Sciences, Queen Mary University of London, London, E1 4NS, United Kingdom.*

**GABRIEL YVON-DUROCHER,** *School of Biological & Chemical Sciences, Queen Mary University of London, London,E1 4NS, United Kingdom.*

# Preface

## Ecological Networks: Simple Rules for Complex Systems in a Changing World?

This Thematic Volume of *Advances in Ecological Research* is dedicated to the study of ecological networks—the webs of antagonistic or mutualistic interactions that occur between individuals and, ultimately, also at the higher levels of biological organisation (e.g. among species populations or size-classes). Darwin first employed the metaphor of the '*entangled bank*' to describe a network of interacting species in the *Origin of Species* in 1859, and the first recognisable ball-and-stick diagram of a food web was described by Camerano (1880) a couple of decades later. Many of the eminent pioneering ecologists of their day also turned their attention to these systems, including Elton (1927), Lindeman (1942), MacArthur (1955), and Hutchinson (1959), who were among the first to suggest that complexity might confer stability on natural systems and that body size plays a key role in structuring communities and in determining the strength of interactions. These early ideas linking complexity to stability were subsequently challenged by the seminal modelling work of May (1972, 1973) and many others, who demonstrated mathematically that complexity should decrease stability. This raised the long-standing question as to what might be the '*devious strategies*' that allow the complex food webs we see in nature to persist. A new generation of food webs that were constructed with far greater sampling effort and better taxonomic resolution appeared from the 1990s onwards, in conjunction with new mathematical models that demonstrated how complex systems could be stable—for instance, if most links were weak (e.g. McCann, Hastings and Huxel, 1998). Since then, numerous studies have demonstrated, both empirically and theoretically, that the body-size of consumers and their resources is a key determinant of interaction strength, network structure and stability (e.g. Berlow *et al.*, 2009; Emmerson and Raffaelli, 2004).

In the last two decades, the study of ecological networks has undergone a dramatic renaissance, which has been manifested by the opening of new research vistas and an exponential rise in the number of publications (Ings *et al.*, 2009). The catalogue of high-quality data has now grown sufficiently for ecologists to be able to undertake meaningful meta-analysis and to search for macroecological patterns in network structure and dynamics across a wide range of systems, two areas that had, until recently, been hampered by limited or inconsistent data collection, as highlighted by the paper by Riede and co-authors in this Volume. In addition, the study of 'traditional' food webs and host–parasitoid networks has been complemented by the recent blossoming of research into mutualistic networks (e.g. plant–pollinator webs) and the attendant cross-fertilisation of ideas emerging from the study of networks in the social sciences, which are covered in Olesen *et al.*'s comprehensive review and synthesis paper. We are now edging closer to being able to make some (fairly) firm generalisations about network structure and dynamics, and to start to build predictive frameworks to anticipate how they might respond to natural and anthropogenic perturbations. One recurrent theme that has (re)emerged in recent years and that runs through much of this Volume and echoes the ideas of the early ecologists, particularly those of Elton and Hutchinson, is that body size plays a key role (e.g. Cohen *et al.*, 2003) and that its correlates (e.g. basal metabolic rate) have effects that can ramify through the food web.

The first paper in the Volume (Olesen *et al.*, 2010) provides an overview of the current and emerging perspectives in eight key areas of network research, including an in-depth consideration of the structuring of networks, and how this varies with both space and time. In the second paper, by Woodward *et al.* (2010), a new theoretical framework, based on first-principles related primarily to metabolic constraints and ecological stoichiometry, is suggested as a possible means of developing a more mechanistic understanding of network-level responses to climate change. The subsequent papers are based on detailed empirical data from a range of different systems, including marine, freshwater and terrestrial food webs. The first of these, by Riede *et al.* (2010), is a meta-analysis of network properties using a new, high-quality dataset, which reveals strong evidence of power-law scaling between network size and a range of food web parameters. The paper by McLaughlin *et al.* (2010) explores network properties and size-structuring within a highly resolved terrestrial above- and below-ground food web. The penultimate paper, by Layer *et al.* (2010) is a macroecological and modelling study of 20 stream food webs across a wide pH gradient, and is one of the first attempts to understand how structure and stability of networks is shaped by an environmental stressor. The final paper, by O'Gorman and Emmerson (2010), considers the role of body size within a benthic marine food web, and represents one of the first studies to characterise highly resolved networks within a replicated field experiment. In summary, the six papers that comprise this Volume cover a wide range of ecosystems (marine, freshwater and terrestrial), network types (food webs, mutualistic and host–parasitoid networks) and also combine theoretical and empirical approaches. Although the role of body size is addressed in each contribution, this does not in any way imply that it is the sole variable of interest or importance, but rather it represents a useful principal component that can capture much of the biologically relevant variation within a network. Examining the 'residuals about the line' can therefore provide invaluable additional information about a wide range of other important ecological properties and phenomena (e.g. idiosyncratic species traits, adaptive behaviour, and phylogenetic constraints) that would otherwise be masked. In many cases, and especially in aquatic systems, body size provides a relatively simple set of rules that can be used to help understand and (ultimately) predict the structure and dynamics of complex ecological networks and how they might respond to future change. This is a rather daunting, but also exciting, prospect for future ecological research, and the compilation of papers within this Volume represent a step towards this goal.

Guy Woodward

# REFERENCES


Berlow, E.A., Dunne, J.A., Martinez, N.D., Starke, P.B., Williams, R.J., and Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proc. Natl. Acad. Sci. USA* **106**, 187–191.

Camerano, L. (1880). Dell' equilibrio dei viventi mercé la reciproca distruzione. *Atti della Reale Accademia delle Scienze di Torino* **15**, 393–414.

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

Darwin, C. (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.

Elton, C.S. (1927). *Animal Ecology*. Sedgewick and Jackson, London.

Emmerson, M., and Raffaelli, D. (2004). Predator–prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* **73**, 399–409.

Hutchinson, G.E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159.

Ings, T.C., Montoya, J.M., Bascompte, J., Bluthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., , Ledger, M.E. *et al.* (2009). Ecological networks—Beyond food webs. *J. Anim. Ecol.* **78**, 253–269.

Lindeman, R.L. (1942). The trophic–dynamic aspect of ecology. *Ecology* **23**, 399–418.

Layer, K., Riede, J.O., Hildrew, A.G., and Woodward, G. (2010). Food web structure and stability in 20 streams across a wide pH gradient. *Adv. Ecol. Res.* **42**, 267–301.

MacArthur, R. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–536.

May, R.M. (1972). Will a large complex system be stable? *Nature* **238**, 413–414.

May, R.M. (1973). Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.