

Syllabus for Ecosystem Ecology (PCB 5338)**Credit hours:** 3, graded.**Instructor:** Jeremy Lichstein**Office hours:** by appointment in 317 Carr Hall**Class time/location:**

Monday periods 6-7 (12:50-2:45) in 521 Carr Hall.

Friday period 4 (10:40-11:30) in 222 Carr Hall.

Course Description

We will learn about the basic principles that govern the structure and function of ecosystems, with an emphasis on carbon and nutrient cycling in the context of climate change and other global change drivers (e.g., nitrogen deposition, land use change, and altered disturbance regimes). Examples of the questions we will seek to answer include: How is ecosystem carbon storage responding to climate change? How do ecosystem-atmosphere feedbacks affect climate? How do ecosystems respond to elevated atmospheric CO₂ concentrations, and how does nutrient availability affect this CO₂ response? How does biodiversity affect ecosystem function? We will cover both fundamental principles and recent, cutting-edge research. Most of the semester will focus on terrestrial ecosystems, but we will also include discussions of freshwater and marine systems to gain a holistic and global perspective on ecosystem ecology.

Please use Canvas Mail for all course-related emails.**Format**

- Typically, 1 period per week will be reserved for lecture, and 2 periods for class discussions of journal articles.
- We will typically read/discuss the equivalent of two full-length (e.g., 10 page) papers per week.
- Some journal article discussions will be led by student teams (2 students), and some will be instructor-led.
- Each journal discussion will begin with a brief (5 minute) presentation by the discussion leader(s) followed by question/answer. The goals of the presentation and Q/A are to help everyone understand the main points of the paper. Discussion leaders should *not* feel pressure to be able to answer every question, or to understand all technical details in the paper. We will work as a group to understand the papers, and it is OK for discussion leaders to bring their own questions to the class. Following Q/A, we will have a group discussion to explore the paper more deeply, including understanding the context of the paper (why is it important?) and critically evaluating if the authors' conclusions are supported by their results.
- Homework is due one hour before each class, unless stated otherwise. See details below under 'Reading Assignments' and 'Homework Assignments'.

Textbook

There is no required textbook. Required readings will be journal articles or other readings you can download for free. If you want to do some background reading on your own, a recommended text is *Principles of Terrestrial Ecosystem Ecology* by Chapin et al. Two editions have been printed. Used copies of the first edition are available for about \$15.

Reading assignments

Carefully read each assigned paper. Most full-length papers will require *at least one hour* of careful reading and thinking. You are not expected to understand every detail, but you should aim to understand the context (why is the paper important?) and main points. If there are unfamiliar terms that prevent you from grasping the context and main points, then you should look these terms up. I have found Wikipedia to be pretty reliable for getting a quick understanding of most scientific terms and concepts. You do not need to read supplementary sections of papers (Appendixes, Supplementary Material, etc.) unless these are specifically assigned.

Homework assignments (due one hour before each class unless stated otherwise)

Homework should be written *in your own words*. Please do not quote directly from sources (except for technical terms or phrases). For each assigned paper, you should upload a written assignment to Canvas with four sections labeled as follows:

1. **Main points.** Write a few sentences summarizing the main points. [Or if you feel you did not understand the main points, explain why you got stuck. If convenient, you can simply refer to #3 below.]
2. **Significance.** A single sentence of the form “This paper is important because...” [Or if you disagree, you can write “This paper is *not* important because...”]
3. **Understanding.** If there are topics in the paper you need help understanding or would like to learn more about, please describe *up to three* topics or questions.
4. **Class discussion.** Describe a topic or question related to the paper that you think would be interesting for the class to discuss.

Assessments and grading

There will be no exams or quizzes. The grade breakdown will be:

- **20%: Leading discussions.** Each student will co-lead several discussions.
- **40%: Participation.** Each student is expected to participate in all discussions.
- **40%: Homework.** Homework is typically due one hour prior to each class meeting and should be submitted to Canvas/Assignments. If you miss class, you are still expected to submit homework on time, unless circumstances (e.g., illness) prevent you from doing so (in which case you should notify the instructor). Homework can be submitted up to one week late, but will be flagged as ‘late’. Multiple instances of late or missing homework will result in a semester grade reduction.

Absences

Please notify the instructor ahead of time if you plan to miss class. Absences will be excused according to standard UF policies (illness, religious holidays, etc.) and for academic/research-related reasons (attending conferences, job interviews, etc.). You are welcome to discuss excused absences with the instructor in person, but you should always send a written explanation by email so that there is a record of the excused absence (remember to use Canvas Mail for all course-related matters).

Schedule of topics and readings

- **Assigned-S** = student-led discussion.
- **Assigned-I** = instructor-led discussion.
- **Further reading** = suggested (optional) readings if you want to dig deeper.

Week 1

Monday Jan. 8: pre-test

Friday Jan. 12: Net primary production (NPP)

Assigned-I: (Field *et al.* 1998)

Further reading: (Clark *et al.* 2001; Malhi *et al.* 2009, 2011)

Week 2

Monday Jan. 15: MLK day

Friday Jan. 19: Biodiversity and ecosystem functioning

Assigned-I: (Tilman *et al.* 2006a)

Further reading on biofuels: (Hill *et al.* 2006; Fargione *et al.* 2008; Searchinger *et al.* 2008; Tilman *et al.* 2009)

Further reading on net ecosystem production (NEP) and net ecosystem carbon balance (NECB): (Olson 1963; Odum 1969; Baldocchi *et al.* 2001; Baldocchi 2003; Chapin *et al.* 2006)

Week 3

Monday Jan. 22: Biodiversity and ecosystem functioning

Assigned-S: (Hooper & Vitousek 1997)

Further reading: (Doak *et al.* 1998; Hooper *et al.* 2005, 2012; Tilman *et al.* 2006b; Cardinale *et al.* 2012; Isbell *et al.* 2015; Sakschewski *et al.* 2016)

Friday Jan. 26: Biodiversity and ecosystem functioning

Assigned-S: (Huston 1997)

Week 4

Monday Jan. 29: Transfer of energy and matter across trophic levels

Assigned-I: (Lindeman 1942)

Further reading: (Tansley 1935; Odum 1957)

Friday Feb. 2: Disturbance and ecosystem C storage

Assigned-S: (Harmon 2001)

Further reading on C storage across spatial/temporal scales: (Smithwick *et al.* 2007)

Week 5

Monday Feb. 5: Disturbance and ecosystem C storage

Assigned-S: (Campbell *et al.* 2012; Hurteau *et al.* 2016)

Further reading on extreme events: (Kurz *et al.* 2008; Reichstein *et al.* 2013; Frank *et al.* 2015; Bradford & Bell 2017; Stevens-Rumann *et al.* 2017). A useful exercise is to look at how Pan *et al.* (2011b) calculate regional totals for NEP in their Table 3. Do their calculations account for the C lost from the ecosystem due to disturbance (conversion of a regrowing or mature forest to an age-zero forest)?

Friday Feb. 9: Disturbance and ecosystem carbon storage (continued)

Assigned-S: (Harmon *et al.* 1990)

Further reading on how land use affects atmospheric C: (Marland & Marland 1992; Marland & Schlamadinger 1997; Canadell & Raupach 2008; Searchinger *et al.* 2008)

Week 6

Monday Feb. 12: Nutrient limitation in terrestrial ecosystems

Assigned-S: (Chapin *et al.* 1986)

Further reading: (Chadwick *et al.* 1999; Hedin *et al.* 2003; Hungate *et al.* 2003; Luo *et al.* 2004; Barron *et al.* 2009; Norby *et al.* 2010; Wright *et al.* 2011)

Friday Feb. 16

Assigned-S: (Vitousek & Howarth 1991)

Further reading on nitrogen fixation and associated paradoxes: (Menge *et al.* 2009a, 2014)

Week 7

Monday Feb. 19: Nutrient cycling in terrestrial ecosystems

Assigned-S: (Crews *et al.* 1995)

Friday Feb. 23: Nutrient cycling in terrestrial ecosystems

Assigned-S: (Hedin *et al.* 1995)

Further reading on models of nutrient cycling. These papers use models to gain important insights into how nutrient cycling operates in ecosystems:

- Parton *et al.* (1987) describe the widely-used CENTURY model for terrestrial biogeochemical cycling. Subsequent papers by Parton *et al.* further develop the model and apply it to different terrestrial ecosystems.
- Bolker and Pacala (1998): insightful analysis of the CENTURY model.
- Menge *et al.* (2009b) develop a model for N and P cycling across different time scales.
- Dybzinski *et al.* (2011) derive a clever simplification of a model of N cycling (see their Appendix G), and use their simplified model to derive optimal allocation strategies for plants competing for light and N.

Week 8

Monday Feb. 26: Isotope methods and applications in ecosystem ecology

Assigned-I: (Robinson 2001)

Friday March 2: Isotope methods and applications in ecosystem ecology

Assigned-I: (Trumbore 2000)

Further reading: (Nadelhoffer *et al.* 1999; Cernusak *et al.* 2013; Pries *et al.* 2013)

Week 9

Monday March 12: Dynamics of soil organic matter

Assigned-I: (Schmidt *et al.* 2011)

Further reading: (Olson 1963; Kuzyakov 2006, 2010)

Friday March 16: Fungal effects on soil organic matter

Assigned-S: (Fernandez & Kennedy 2016)

Week 10

Monday March 19: High latitude terrestrial ecosystems – *Guest lecture with PhD candidate Jack Hutchings*

Assigned-I: (Mauritz *et al.* 2017)

Further reading: (Schoor *et al.* 2008; Schoor & Abbott 2011)

Friday March 23: Ecosystem metabolism in flowing waters – *Guest lecture with Dr. Matt Cohen*

Assigned-I: (Odum 1956; Bernhardt *et al.* 2017)

Week 11

Monday March 26: Carbon and nutrient cycling in freshwater wetlands – *Guest lecture with Dr. Todd Osborne*

Assigned-I: TBA

Friday March 30: Eutrophication in flowing waters – *Guest lecture with Dr. Matt Cohen*

Assigned: none

Further reading: (Bianchi *et al.* 2010)

Week 12

Monday April 2: Carbon sequestration in coastal ecosystems – *Guest lecture with Dr. Tom Bianchi*

Assigned-I: (Bauer *et al.* 2013)

Further reading: (Bianchi 2011)

Friday April 6: Global ocean C sink

Assigned-I: Section 7.3.4 (pp. 528-533) of Denman *et al.* (2007)

Further reading (role of viruses in the ocean C cycle): (Fuhrman 1999; Wilhelm & Suttle 1999; Suttle 2005; Danovaro *et al.* 2011; Weitz & Wilhelm 2012). Note that the Suttle (2005) paper is widely cited, but the paper misrepresents the global C cycle (e.g., Fig. 4 ignores the land C sink, and incorrectly attributes the entire ocean C sink to sinking particulate organic matter).

Week 13

Monday April 9: Biogeochemistry of seagrass beds – *Guest lecture with PhD candidate Robert Johnson*

Assigned-I: (Johnson *et al.* 2017)

Friday April 13: Managing seagrass beds for C sequestration

Assigned-S: (Johannessen & Macdonald 2016)

Week 14

Monday April 16 paper discussion: Nutrient subsidies from terrestrial to aquatic ecosystems

Assigned-S: (Subalusky *et al.* 2017)

Further reading: (Carpenter *et al.* 2005; Subalusky *et al.* 2015)

Monday April 16 lecture: Global C cycle

Further reading (land and ocean C sinks): (Tans *et al.* 1990; Canadell *et al.* 2007; Le Quere *et al.* 2009; Pan *et al.* 2011a; Schimel *et al.* 2015)

Further reading (dynamic global vegetation models): (Foley *et al.* 1996; Scheiter *et al.* 2013)

Further reading (Earth system models): (Bonan & Doney 2018)

Friday April 20: Drought sensitivity of tropical forest C balance

Assigned-S: (Phillips *et al.* 2009)

Week 15

Monday April 23 (last class): Are old-growth tropical forests a C sink?

Assigned-I: (Chambers *et al.* 2013)

Further reading: (Fisher *et al.* 2008; Gloor *et al.* 2009; Wright 2013; Brienen *et al.* 2015)

References

- Baldocchi, D., Falge, E., Gu, L.H., Olson, R., Hollinger, D., Running, S., *et al.* (2001). FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull. Am. Meteorol. Soc.*, 82, 2415–2434.
- Baldocchi, D.D. (2003). Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Glob. Change Biol Glob. Change Biol*, 9, 479–492.
- Barron, A.R., Wurzbarger, N., Bellenger, J.P., Wright, S.J., Kraepiel, A.M.L. & Hedin, L.O. (2009). Molybdenum limitation of asymbiotic nitrogen fixation in tropical forest soils. *Nat. Geosci.*, 2, 42–45.
- Bauer, J.E., Cai, W.-J., Raymond, P.A., Bianchi, T.S., Hopkinson, C.S. & Regnier, P.A.G. (2013). The changing carbon cycle of the coastal ocean. *Nature*, 504, 61–70.
- Bernhardt, E.S., Heffernan, J.B., Grimm, N.B., Stanley, E.H., Harvey, J.W., Arroita, M., *et al.* (2017). The metabolic regimes of flowing waters. *Limnol. Oceanogr.*, 1–20.
- Bianchi, T.S. (2011). The role of terrestrially derived organic carbon in the coastal ocean: A changing paradigm and the priming effect. *Proc. Natl. Acad. Sci. U. S. A.*, 108, 19473–19481.
- Bianchi, T.S., DiMarco, S.F., Cowan, J.H., Hetland, R.D., Chapman, P., Day, J.W., *et al.* (2010). The science of hypoxia in the Northern Gulf of Mexico: A review. *Sci. Total Environ.*, 408, 1471–1484.
- Bolker, B., Pacala, S. & Parton, W. (1998). Linear analysis of soil decomposition: Insights from the CENTURY model. *Ecol. Appl.*, 8, 425–439.
- Bonan, G.B. & Doney, S.C. (2018). Climate, ecosystems, and planetary futures: The challenge to predict life in Earth system models. *Science*, 359, in press.
- Bradford, J.B. & Bell, D.M. (2017). A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. *Front. Ecol. Environ.*, 15, 11–17.
- Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., *et al.* (2015). Long-term decline of the Amazon carbon sink. *Nature*, 519, 344–348.
- Campbell, J.L., Harmon, M.E. & Mitchell, S.R. (2012). Can fuel-reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? *Front. Ecol. Environ.*, 10, 83–90.
- Canadell, J.G., Le Quere, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., *et al.* (2007). Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proc. Natl. Acad. Sci.*, 104, 18866–18870.
- Canadell, J.G. & Raupach, M.R. (2008). Managing forests for climate change mitigation. *Science*, 320, 1456–1457.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.
- Carpenter, S.R., Cole, J.J., Pace, M.L., Van de Bogert, M., Bade, D.L., Bastviken, D., *et al.* (2005). Ecosystem subsidies: Terrestrial support of aquatic food webs from C-13 addition to contrasting lakes. *Ecology*, 86, 2737–2750.
- Cernusak, L.A., Ubierna, N., Winter, K., Holtum, J.A.M., Marshall, J.D. & Farquhar, G.D. (2013). Environmental and physiological determinants of carbon isotope discrimination in terrestrial plants. *New Phytol.*, 200, 950–965.
- Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J. & Hedin, L.O. (1999). Changing sources of nutrients during four million years of ecosystem development. *Nature*, 397, 491–497.
- Chambers, J.Q., Negrón-Juarez, R.I., Marra, D.M., Di Vittorio, A., Tews, J., Roberts, D., *et al.* (2013). The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proc. Natl. Acad. Sci. U. S. A.*, 110, 3949–3954.
- Chapin, F.S., Vitousek, P.M. & Vanclve, K. (1986). The nature of nutrient limitation in plant communities. *Am. Nat.*, 127, 48–58.

- Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., *et al.* (2006). Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*, 9, 1041–1050.
- Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R. & Ni, J. (2001). Measuring net primary production in forests: Concepts and field methods. *Ecol. Appl.*, 11, 356–370.
- Crews, T.E., Kitayama, K., Fownes, J.H., Riley, R.H., Herbert, D.A., Mueller-Dombois, D., *et al.* (1995). Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology*, 76, 1407–1424.
- Danovaro, R., Corinaldesi, C., Dell’Anno, A., Fuhrman, J.A., Middelburg, J.J., Noble, R.T., *et al.* (2011). Marine viruses and global climate change. *Fems Microbiol. Rev.*, 35, 993–1034.
- Denman, K.L., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P.M., Dickinson, R.E., *et al.* (2007). Couplings Between Changes in the Climate System and Biogeochemistry. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds. Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., *et al.*). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 499–587.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O’Malley, R.E. & Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.*, 151, 264–276.
- Dybzinski, R., Farrior, C., Wolf, A., Reich, P.B. & Pacala, S.W. (2011). Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. *Am. Nat.*, 177, 153–166.
- Fargione, J., Hill, J., Tilman, D., Polasky, S. & Hawthorne, P. (2008). Land clearing and the biofuel carbon debt. *Science*, 319, 1235–1238.
- Fernandez, C.W. & Kennedy, P.G. (2016). Revisiting the “Gadgil effect”: do interguild fungal interactions control carbon cycling in forest soils? *New Phytol.*, 209, 1382–1394.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T. & Falkowski, P. (1998). Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science*, 281, 237–240.
- Fisher, J.I., Hurtt, G.C., Thomas, R.Q. & Chambers, J.Q. (2008). Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecol. Lett.*, 11, 554–563.
- Foley, J.A., Prentice, I.C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., *et al.* (1996). An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Glob. Biogeochem. Cycles*, 10, 603–628.
- Frank, D.A., Reichstein, M., Bahn, M., Thonicke, K., Frank, D., Mahecha, M.D., *et al.* (2015). Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. *Glob. Change Biol.*, 21, 2861–2880.
- Fuhrman, J.A. (1999). Marine viruses and their biogeochemical and ecological effects. *Nature*, 399, 541–548.
- Gloor, M., Phillips, O.L., Lloyd, J.J., Lewis, S.L., Malhi, Y., Baker, T.R., *et al.* (2009). Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? *Glob. Change Biol.*, 15, 2418–2430.
- Harmon, M.E. (2001). Carbon sequestration in forests: Addressing the scale question. *J. For.*, 99, 24–29.
- Harmon, M.E., Ferrell, W.K. & Franklin, J.F. (1990). Effects on carbon storage of conversion of old-growth forests to young forests. *Science*, 247, 699–702.
- Hedin, L.O., Armesto, J.J. & Johnson, A.H. (1995). Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. *Ecology*, 76, 493–509.
- Hedin, L.O., Vitousek, P.M. & Matson, P.A. (2003). Nutrient losses over four million years of tropical forest development. *Ecology*, 84, 2231–2255.

- Hill, J., Nelson, E., Tilman, D., Polasky, S. & Tiffany, D. (2006). Environmental, economic, and energetic costs and benefits of biodiesel and ethanol biofuels. *Proc. Natl. Acad. Sci. U. S. A.*, 103, 11206–11210.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., *et al.* (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486, 105–108.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.
- Hooper, D.U. & Vitousek, P.M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, 277, 1302–1305.
- Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y. & Field, C.B. (2003). Nitrogen and climate change. *Science*, 302, 1512.
- Hurteau, M.D., Liang, S., Martin, K.L., North, M.P., Koch, G.W. & Hungate, B.A. (2016). Restoring forest structure and process stabilizes forest carbon in wildfire-prone southwestern ponderosa pine forests. *Ecol. Appl.*, 26, 382–391.
- Huston, M.A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., *et al.* (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577.
- Johannessen, S.C. & Macdonald, R.W. (2016). Geoengineering with seagrasses: is credit due where credit is given? *Environ. Res. Lett.*, 11, 113001.
- Johnson, R.A., Gulick, A.G., Bolten, A.B. & Bjorndal, K.A. (2017). Blue carbon stores in tropical seagrass meadows maintained under green turtle grazing. *Sci. Rep.*, 7, 13545.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., *et al.* (2008). Mountain pine beetle and forest carbon feedback to climate change. *Nature*, 452, 987–990.
- Kuzyakov, Y. (2006). Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biol. Biochem.*, 38, 425–448.
- Kuzyakov, Y. (2010). Priming effects: Interactions between living and dead organic matter. *Soil Biol. Biochem.*, 42, 1363–1371.
- Le Quere, C., Raupach, M.R., Canadell, J.G., Marland, G., Bopp, L., Ciais, P., *et al.* (2009). Trends in the sources and sinks of carbon dioxide. *Nat. Geosci.*, 2, 831–836.
- Lindeman, R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23, 399–418.
- Luo, Y., Su, B., Currie, W., Dukes, J., Finzi, A., Hartwig, U., *et al.* (2004). Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, 54, 731–739.
- Malhi, Y., Aragao, L.E.O.C., Metcalfe, D.B., Paiva, R., Quesada, C.A., Almeida, S., *et al.* (2009). Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Glob. Change Biol.*, 15, 1255–1274.
- Malhi, Y., Doughty, C. & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philos. Trans. R. Soc. B-Biol. Sci.*, 366, 3225–3245.
- Marland, G. & Marland, S. (1992). Should we store carbon in trees? *Water. Air. Soil Pollut.*, 64, 181–195.
- Marland, G. & Schlamadinger, B. (1997). Forests for carbon sequestration or fossil fuel substitution? A sensitivity analysis. *Biomass Bioenergy*, 13, 389–397.
- Mauritz, M., Bracho, R., Celis, G., Hutchings, J., Natali, S.M., Pegoraro, E., *et al.* (2017). Nonlinear CO₂ flux response to 7 years of experimentally induced permafrost thaw. *Glob. Change Biol.*, 23, 3646–3666.
- Menge, D.N.L., Levin, S.A. & Hedin, L.O. (2009a). Facultative versus obligate nitrogen fixation strategies and their ecosystem consequences. *Am. Nat.*, 174, 465–477.

- Menge, D.N.L., Lichstein, J.W. & Angeles-Perez, G. (2014). Nitrogen fixation strategies can explain the latitudinal shift in nitrogen-fixing tree abundance. *Ecology*, 95, 2236–2245.
- Menge, D.N.L., Pacala, S.W. & Hedin, L.O. (2009b). Emergence and maintenance of nutrient limitation over multiple timescales in terrestrial ecosystems. *Am. Nat.*, 173, 164–175.
- Nadelhoffer, K.J., Emmett, B.A., Gundersen, P., Kjonaas, O.J., Koopmans, C.J., Schleppei, P., *et al.* (1999). Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature*, 398, 145–148.
- Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E. & McMurtrie, R.E. (2010). CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *Proc. Natl. Acad. Sci. U. S. A.*, 107, 19368–19373.
- Odum, E.P. (1969). The strategy of ecosystem development. *Science*, 164, 262–270.
- Odum, H.T. (1956). Primary production in flowing waters. *Limnol. Oceanogr.*, 1, 102–117.
- Odum, H.T. (1957). Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.*, 27, 55–112.
- Olson, J.S. (1963). Energy storage and balance of producers and decomposers in ecological systems. *Ecology*, 44, 322–331.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., *et al.* (2011a). A large and persistent carbon sink in the world's forests. *Science*, 333, 988–993.
- Pan, Y., Chen, J.M., Birdsey, R., McCullough, K., He, L. & Deng, F. (2011b). Age structure and disturbance legacy of North American forests. *Biogeosciences*, 8, 715–732.
- Parton, W., Schimel, D., Cole, C. & Ojima, D. (1987). Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Soc. Am. J.*, 51, 1173–1179.
- Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., *et al.* (2009). Drought sensitivity of the Amazon rainforest. *Science*, 323, 1344–1347.
- Pries, C.E.H., Schuur, E.A.G. & Crummer, K.G. (2013). Thawing permafrost increases old soil and autotrophic respiration in tundra: Partitioning ecosystem respiration using delta C-13 and Delta C-14. *Glob. Change Biol.*, 19, 649–661.
- Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., *et al.* (2013). Climate extremes and the carbon cycle. *Nature*, 500, 287–295.
- Robinson, D. (2001). delta N-15 as an integrator of the nitrogen cycle. *Trends Ecol. Evol.*, 16, 153–162.
- Sakschewski, B., von Bloh, W., Boit, A., Poorter, L., Pena-Claros, M., Heinke, J., *et al.* (2016). Resilience of Amazon forests emerges from plant trait diversity. *Nat. Clim. Change*, 6, 1032–1036.
- Scheiter, S., Langan, L. & Higgins, S.I. (2013). Next-generation dynamic global vegetation models: learning from community ecology. *New Phytol.*, 198, 957–969.
- Schimel, D., Stephens, B.B. & Fisher, J.B. (2015). Effect of increasing CO₂ on the terrestrial carbon cycle. *Proc. Natl. Acad. Sci. U. S. A.*, 112, 436–441.
- Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., *et al.* (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, 478, 49–56.
- Schuur, E.A.G. & Abbott, B. (2011). High risk of permafrost thaw. *Nature*, 480, 32–33.
- Schuur, E.A.G., Bockheim, J., Canadell, J.G., Euskirchen, E., Field, C.B., Goryachkin, S.V., *et al.* (2008). Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. *BioScience*, 58, 701–714.
- Searchinger, T., Heimlich, R., Houghton, R.A., Dong, F., Elobeid, A., Fabiosa, J., *et al.* (2008). Use of US croplands for biofuels increases greenhouse gases through emissions from land-use change. *Science*, 319, 1238–1240.
- Smithwick, E.A.H., Harmon, M.E. & Domingo, J.B. (2007). Changing temporal patterns of forest carbon stores and net ecosystem carbon balance: The stand to landscape transformation. *Landsc. Ecol.*, 22, 77–94.

- Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D.C., *et al.* (2017). Evidence for declining forest resilience to wildfires under climate change. *Ecol. Lett.*, in press.
- Subalusky, A.L., Dutton, C.L., Rosi, E.J. & Post, D.M. (2017). Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proc. Natl. Acad. Sci. U. S. A.*, 114, 7647–7652.
- Subalusky, A.L., Dutton, C.L., Rosi-Marshall, E.J. & Post, D.M. (2015). The hippopotamus conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. *Freshw. Biol.*, 60, 512–525.
- Suttle, C.A. (2005). Viruses in the sea. *Nature*, 437, 356–361.
- Tans, P.P., Fung, I.Y. & Takahashi, T. (1990). Observational constraints on the global atmospheric CO₂ budget. *Science*, 247, 1431–1438.
- Tansley, A.G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*, 16, 284–307.
- Tilman, D., Hill, J. & Lehman, C. (2006a). Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, 314, 1598–1600.
- Tilman, D., Reich, P.B. & Knops, J.M.H. (2006b). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–632.
- Tilman, D., Socolow, R., Foley, J.A., Hill, J., Larson, E., Lynd, L., *et al.* (2009). Beneficial Biofuels-The Food, Energy, and Environment Trilemma. *Science*, 325, 270–271.
- Trumbore, S. (2000). Age of soil organic matter and soil respiration: Radiocarbon constraints on belowground C dynamics. *Ecol. Appl.*, 10, 399–411.
- Vitousek, P.M. & Howarth, R.W. (1991). Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry*, 13, 87–115.
- Weitz, J.S. & Wilhelm, S.W. (2012). Ocean viruses and their effects on microbial communities and biogeochemical cycles. *F1000 Biol. Rep.*, 4, 1–8.
- Wilhelm, S.W. & Suttle, C.A. (1999). Viruses and Nutrient Cycles in the Sea - Viruses play critical roles in the structure and function of aquatic food webs. *BioScience*, 49, 781–788.
- Wright, S.J. (2013). The carbon sink in intact tropical forests. *Glob. Change Biol.*, 19, 337–339.
- Wright, S.J., Yavitt, J.B., Wurzbarger, N., Turner, B.L., Tanner, E.V.J., Sayer, E.J., *et al.* (2011). Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, 92, 1616–1625.