Temporal Biology Seminar: Phenology

Phenology, the timing of annual life cycle events, is a critical trait in living organisms, influencing and being influenced by evolution and ecology across many scales. In this graduate seminar we will discuss the biological underpinnings and implications of phenology through primary scientific literature.

Course objectives: The goal of this course is for students to broadly consider the role that phenology plays in biological, ecological and evolutionary processes. Specifically, students will:

- Understand the biological and evolutionary underpinnings of phenology.
- Consider the role of phenology in structuring ecological and evolutionary processes.
- Gain exposure to the diverse application of phenological research within the field of biology, and consider phenology's role in their own field of interest.

Course Structure: This seminar will meet once per week for two hours. Meetings will consist of brief introductory and concluding remarks by the instructor and a student facilitated discussion.

Prerequisites: Advanced academic standing with introductory coursework in ecology and evolution, or permission of instructor.

Week	Topic	Lecture Focus	Readings
		Part I: Fundamentals	
Week 1	Introductory Remarks	What is phenology anyway? Is phenology a "trait"?	Forest and Rushing 2010 Lechowicz 1984, Ollerton 1992,
Week 2	Environmental Cues	Environmental factors influencing phenology Modeling phenological responses to environments	Rathke and Lacey 1985 Chuine 2000, Fu 2014
Week 3	Physiology of Phenology	How/Where do plants perceive their environment? Genetic regulation of phenology	Bernier 2005 Wilczek 2010, Visser 2010
Week 4	Evolution of Phenology	Heritability and local adaptation of phenology	Liepe 2016 McDonough-MacKenzie 2018, Vitasse 2009
Week 5	Carryover Effects	Phenological sequences Maternal effects	Gougherty 2018 Johnsen 2005, Auge 2017
		Part II: Function	
Week 6	Ecosystem Ecology	Phenology, fluxes and feedbacks	Richardson 2013 Fitzjarrald 2001, McKown 2012
Week 7	Community Ecology	Temporal Niches Phenology and competition	Fargione 2005 Ross 1972, Wainwright 2011
Week 8	Evolutionary Biology	Phenological speciation: Allochrony Phenology and life history evolution	Taylor 2017 Burghardt 2015, Rubin 2018
		Part III: Phenology in a Changing World	
Week 9	Phenological Shifts	Observed changes	Menzel 2006 Ffrench-Constant 2016, Fu, 2015
Week 10	Invasion	Phenology as a mechanism of invasion Rapid evolution of phenological response	Wolkovich 2013, Gioria 2017 Erfmeier 2005
Week 11	Phenology and Extremes	False Spring Drought	Gu 2008 Ivits 2014, Cui 2017
Week 12	Phenological Mismatches	Pollinator networks Herbivory and predation	Kudo 2003 Kharouba 2015, Petanidou 2014

References

Auge, G.A., Blair, L.K., Neville, H. & Donohue, K. (2017) Maternal vernalization and vernalization-pathway genes influence progeny seed germination. *New Phytologist* **216**, 388–400.

Bernier, G. & Périlleux, C. (2005) A physiological overview of the genetics of flowering time control. *Plant Biotechnology Journal* **3**, 3–16.

Burghardt, L.T., Metcalf, C.J.E., Wilczek, A.M., Schmitt, J. & Donohue, K. (2015) Modeling the influence of genetic and environmental variation on the expression of plant life cycles across landscapes. *The American Naturalist* **185**, 212–227.

Chuine, I. (2000) A unified model for budburst of trees. *Journal of Theoretical Biology* **207**, 337 – 347.

Cui, T., Martz, L. & Guo, X. (2017) Grassland phenology response to drought in the canadian prairies. *Remote Sensing* **9**, 1258.

Erfmeier, A. & Bruelheide, H. (2005) Invasive and native Rhododendron ponticum populations: is there evidence for genotypic differences in germination and growth? *ECOGRAPHY* **28**, 417–428.

Fargione, J. & Tilman, D. (2005) Niche differences in phenology and rooting depth promote coexistence with a dominant c4 bunchgrass. *Oecologia* **143**, 598–606.

ffrench Constant, R.H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A. & McGregor, P.K. (2016) Light pollution is associated with earlier tree budburst across the united kingdom. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20160813.

Fitzjarrald, D.R., Acevedo, O.C. & Moore, K.E. (2001) Climatic consequences of leaf presence in the eastern united states. *Journal of Climate* **14**, 598.

Forrest, J. & Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3101–3112.

Fu, Y., Zhang, H., Dong, W. & Yuan, W. (2014) Comparison of phenology models for predicting the onset of growing season over the northern hemisphere. *PLoS ONE* **9**, e109544.

Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas, J. & et al. (2015) Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–107.

Gaku, K. & Y., I.T. (2013) Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* **94**, 2311–2320.

Gioria, M. & Pyšek, P. (2016) Early bird catches the worm: germination as a critical step in plant invasion. *Biological Invasions* **19**, 1055–1080.

Gougherty, A.V. & Gougherty, S.W. (2018) Sequence of flower and leaf emergence in deciduous trees is linked to ecological traits, phylogenetics, and climate. *New Phytologist* **220**, 121–131.

Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008) The 2007 eastern us spring freeze: Increased cold damage in a warming world? *BioScience* **58**, 253–262.

Ivits, E., Horion, S., Fensholt, R. & Cherlet, M. (2013) Drought footprint on european ecosystems between 1999 and 2010 assessed by remotely sensed vegetation phenology and productivity. *Global Change Biology* **20**, 581–593.

Johnsen, Ø., Fossdal, C.G., Nagy, N., Molmann, J., Dæhlen, O.G. & Tore, S. (2005) Climatic adaptation in picea abies progenies is affected by the temperature during zygotic embryogenesis and seed maturation. *Plant, Cell & Environment* **28**, 1090–1102.

Kharouba, H.M., Vellend, M., Sarfraz, R.M. & Myers, J.H. (2015) The effects of experimental warming on the timing of a plant-insect herbivore interaction. *Journal of Animal Ecology* **84**, 785–796.

Lechowicz, M.J. (1984) Why do temperate deciduous trees leaf out at different times? adaptation and ecology of forest communities **124**, 821–842.

Liepe, K.J., Hamann, A., Smets, P., Fitzpatrick, C.R. & Aitken, S.N. (2016) Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. *Evolutionary Applications* **9**, 409–419.

McDonough MacKenzie, C., Primack, R.B. & Miller-Rushing, A.J. (2018) Local environment, not local adaptation, drives leaf-out phenology in common gardens along an elevational gradient in acadia national park, maine. *American Journal of Botany* **105**, 986–995.

McKown, A.D., Guy, R.D., Azam, M.S., Drewes, E.C. & Quamme, L.K. (2012) Seasonality and phenology alter functional leaf traits. *Oecologia* **172**, 653–665.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kumbler, K., Peter, B., Braslavska, O., Briede, A. & et al. (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**, 1969–1976.

Ollerton, J. & Lack, A. (1992) Flowering phenology: An example of relaxation of natural selection? *Trends in Ecology / Evolution* **7**, 274 – 276.

Petanidou, T., Kallimanis, A.S., Sgardelis, S.P., Mazaris, A.D., Pantis, J.D. & Waser, N.M. (2014) Variable flowering phenology and pollinator use in a community suggest future phenological mismatch. *Acta Oecologica* **59**, 104 – 111.

Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**, 179–214.

Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* **169**, 156 – 173.

Ross, M.A. & Harper, J.L. (1972) Occupation of biological space during seedling establishment **60**, 77–88.

Rubin, M.J. & Friedman, J. (2018) The role of cold cues at different life stages on germination and flowering phenology. *American Journal of Botany* **105**, 749–759.

Taylor, R.S. & Friesen, V.L. (2017) The role of allochrony in speciation. *Molecular Ecology* **26**, 3330–3342.

Visser, M.E., Caro, S.P., van Oers, K., Schaper, S.V. & Helm, B. (2010) Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3113–3127.

Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R. & Kremer, A. (2009) Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Canadian Journal of Forest Research* **39**, 1259–1269.

Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2011) Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *Journal of Applied Ecology* **49**, 234–241.

Wilczek, A.M., Burghardt, L.T., Cobb, A.R., Cooper, M.D., Welch, S.M. & Schmitt, J. (2010) Genetic and physiological bases for phenological responses to current and predicted climates. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3129–3147.

Wolkovich, E.M., Davies, T.J., Schaefer, H., Cleland, E.E., Cook, B.I., Travers, S.E., Willis, C.G. & Davis, C.C. (2013) Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany* **100**, 1407–1421.