

Towards a causal understanding of the relationship between structural complexity, productivity and adaptability of forests based on principles of thermodynamics

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Abstract

Managing forests for increased structural complexity as well as acknowledging them as ‘complex adaptive systems’ has become a paradigm in modern silviculture. Primary forests usually show greater structural complexity than managed forests since forest management often aims for several reasons at less complex but specific structures, e.g. for the production of desired wood assortments. Therefore, the question why natural forests seem to gravitate towards maximum structural complexity, at least aboveground, remains. Here we argue that the consideration of thermodynamic theory in forest ecosystem research holds great potential for a deeper understanding as to why structural complexity is beneficial to forests when it comes to evolutionary adaptation. We bring together several existing theories and highlight how structural complexity relates to thermodynamic principles and correspondingly forest productivity, potentially also providing us a means to quantify forests’ adaptive capacity.

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Keywords: forest, exergy, complexity, entropy, buffer capacity

Introduction

The structural complexity of a forest can be defined as all dimensional, architectural, and distributional patterns of plant individuals and their organs in a given space at a given point in time (Seidel et al. 2020). Today, it is possible to quantify the complexity of forest structures objectively, holistically, and efficiently based on light detection and ranging (LiDAR) technology (e.g. Ehbrecht et al. 2021, Heidenreich and Seidel 2022). Structural complexity in general was shown to have beneficial effects on various ecosystem functions and services provided by forests (Lindenmayer et al. 2000, Knoke and Seifert 2008, D’Amato et al. 2011,

Neill and Puettmann 2013). Therefore, managing forests for increased structural complexity and for its maintenance, as well as acknowledging them as ‘complex adaptive systems’ (Holland 1992, Gell-Man and Lloyd 1996, Levin 2003) has become a paradigm in modern silviculture in many countries (Messier et al. 2013). In fact, Möller (1922) who developed the idea of a ‘continuous cover’ forest management had predicted such beneficial effects already 100 years ago (Ammer 2021). Interestingly, there is solid quantitative evidence that, all others things being equal, primary forests possess (on average) a greater structural complexity than managed forests. This was shown for temperate coniferous forests (e.g. Seidel et al. 2016), temperate deciduous forests (e.g. Stiers et al. 2018, 2020), tropical forests (Camaretta et al. 2021), and also boreal forests (Kuuluvainen et al. 1996), but on different absolute levels of structural complexity. Some forests have been explicitly managed for high vertical and horizontal as well compositional heterogeneity over decades and provide a largely uneven-aged structure (Heliwell 1997, Stiers et al. 2020). Such stands can possess high structural complexity, approaching that observed for primary forests (Stiers et al. 2020). Beside management, the absolute level of above-ground structural complexity is determined by the abiotic environment. For example, it was shown that structural complexity of primary forests on global scale strongly increases with the available water (Ehbrecht et al. 2021). Therefore, the global pattern in forest complexity clearly peaks in the tropics, drops drastically to the subtropics, rises strongly towards the temperate zone and finally flattens out at the polar regions (Ehbrecht et al. 2021). Water availability and sufficient time to spatially arrange plant tissue without major disturbance can therefore be described as critical factors for a high structural complexity in forest systems.

While forest management aims at a specific stand structure according to the management goal, the question remains why natural forests seem to gravitate towards maximum structural complexity, at least aboveground. To answer this, it might be helpful to see forests through the lens of thermodynamic theory.

Forests through the lens of thermodynamics

Already 30 years ago, scientists argued that it might be a promising endeavor to apply the principles of thermodynamics to ecosystems (Jørgensen 1990, 1992, Abel and Trevors 2006). Originally developed to describe the energy budgets in closed systems, thermodynamic theory was never utilized to help understanding tree or forest structural complexity.

The first law of thermodynamic states that in a closed system, energy cannot be created or destroyed, it can only be converted from one form to another (Clausius 1850). The second law of thermodynamics tells us that in a closed system, entropy can never be eliminated, it can only remain steady or increase (Clausius 1854). In such a system, all processes therefore result in the conversion of higher-quality energy to lower-quality energy and heat production. This change in energy quality is unidirectional (only from high to low quality) and describes a decreasing availability of exergy, which is that part of energy that can be used to do actual ‘work’ (Nielsen et al. 2020). Brillouin (1960) already described this descending quality of energy from high quality with low entropy (e.g. radiation) to low quality with high entropy (heat). From this, it is obvious that the *non-living* physical world, for which the laws of thermodynamics have been developed, inevitably runs into a condition of maximized entropy, with entropy being best defined as the “level of dissipation that already happened” (cf. Nielsen et al. 2020). Anything that could have happened already happened at the end of this development, all energy will have been converted to heat. However, it is known since more than 100 years (e.g. Lotka 1922) that this does not hold for *living* systems, like plants.

Living organisms are able to make use of external energy sources to power their own biophysical processes, basically to sustain their own life, through the creation of structures in the form of complex molecules (Lotka 1922, Fonseca et al. 2002, Ludovisi 2014). Here, mechanisms involve energy trapping, transduction and storage or immediate utilization for cellular work (Abel and Trevors 2006). Nielsen et al. (2020) stated that the key question is therefore how the thermodynamic balances are handled by living organisms to allow for the build-up of ordered and efficient structures. It was proposed that living systems exploit an energy source (e.g. light) as effectively as possible to maximize the intake of energy (here: exergy or eco-exergy; e.g. Fonseca et al. 2002) in their system to be used for their own processes and in order to create their own structures which are necessary to support the biochemical processes (*sensu* Lotka 1922). Thereby, the

metabolism of living organisms never violates the second law of thermodynamics (Abel and Trevors 2006). Through the utilization and storage however, living systems delay the process of entropy production, often referred to as the creation of anentropy or negentropy (Schrödinger 1944, Nicolis and Prigogine 1971, Nielsen et al. 2020). This was proposed to serve as handy criteria to define what life is (cf. Nielsen et al. 2020) and earlier, to express what evolution might strive for, i.e. energy efficiency and maximized energy throughflow (Lotka 1922).

The first implication of this, when applied to forest ecosystems, is rather trivial: the energy provided by the sun can be interpreted as the fundamental source for the development of forest structures. The second one is less trivial, since one can derive from the above said that forests might actually develop complex structures to enable an efficient use of sunlight (cf. Odum and Pinkerton 1955, Schneider and Kay 1994). If complex structures allow using light as energy source as efficiently as possible on the way between the forest top and the ground floor, structural complex forest have more aboveground resources available to be invested in growth, defense, storage, adaptation or reproduction. Some evidence for this hypothesis exists, since it could be shown that net primary productivity of forests is positively correlated with structural complexity (Harthun 2017, Gough et al. 2019). For trees, a positive relationship between the structural complexity and growth efficiency (wooden tree volume to crown surface area) was discovered (Seidel et al. 2019), as well as a positive relationship between the structural complexity and the productivity of individual trees across more than 40 species (Seidel 2018, Seidel et al. 2019, Dorji et al. 2021). However, the primary productivity of the entire ecosystem (forest) is still difficult to quantify, since it is not possible to quantify belowground productivity well enough. Even for the aboveground parts of a forest, inventories usually do not consider trees smaller than 7 cm in diameter at breast height.

Structural complexity and productivity

In literature, there is a hypothesis as to why forests with high complexity might grow so well: Jørgensen (1992) argued that mature and complex ecosystems, including forests, are able to capture more exergy (usable energy) than immature ecosystems with low complexity. In a study incorporating forests across the eastern United States, it was shown that the fraction of photosynthetically absorbed radiation increases with canopy structural complexity of the stands (Atkins et al. 2018a). Accordingly, when analyzing monocultures and mixed stands, Forrester et al. (2018) found that the light absorption of stands increases as canopy volume increases. The light capturing rate is hypothesized to flatten out when maturity is reached (see Jørgensen 1992) and, in case of a fully stocked mature and unmanaged forest, it likely oscillates around a high level in absence of major disturbances. Since maturity of a forest ecosystem usually corresponds to a larger leaf area per unit ground area, it is not surprising that this measure was shown to relate closely to forest productivity (e.g. Bolstad et al. 2001). However, stand growth depends more directly on light absorption than on leaf area (Binkley et al. 2013). Thus, a given photosynthetically active surface area distributed over a larger vertical extent (multi-layered forest) results not only in a higher structural complexity of the stand when compared to the same leaf area being located in a thin canopy layer (single-layered forest), but possibly also in a higher light absorption and consequently a higher productivity (e.g. Juchheim et al. 2017). Since such multi-layeredness results in more stable microclimate conditions (Ehbrecht et al. 2019), heat loads in the canopy are lower than in single layered stands due to higher exergy uptake. A strongly vertically distributed light absorption and reduced heat loads would also reduce heat stress, and enable efficient photosynthesis which is thermosensitive process (e.g. Wang et al. 2008). In fact, Weigel et al. (2022) stated that it is likely that direct and negative effects of heat on leaf physiology are often underestimated.

Structural complexity and adaptability

Mature (complex) ecosystems are also said to have a higher exergy *storage* when compared to immature (less complex) systems (Jørgensen 1992, Ludovisi 2014). Schneider and Kay (1994), based on data from Luvall and Holbo (1989) provided evidence for this hypothesis based on calculations of the exergy storage derived from remote sensing data of forests in different stages of development. They showed that along the gradient from a quarry without significant amounts of vegetation, through a clear-cut site, a Douglas fir plantation, a natural secondary forest to a 400-year-old Douglas fir-dominated forest the percent of net incoming solar

radiation not used for increasing the system's temperature, increased with the degree of ecosystem maturity. It was argued that biological systems, through the optimization of processes in terms of thermodynamic efficiency, reach a maximized capacity to store exergy, which supposedly translates into a maximized 'buffer capacity' of the system or a maximized ability of the system to adapt to changing conditions (e.g. Mejer and Jørgensen 1979, Jørgensen and Mejer 1981, Jørgensen 2002). If so, this would have important implications for the adaptation of forests to climate change. We hypothesize that structurally complex forests can more easily adapt to changing climate conditions than less complex ones. It remains to be tested whether they are even less vulnerable and thus more resilient to climate changes. However, the buffer capacity and the adaptive capacity (adaptability) do not necessarily mean the same thing. While often used interchangeably in literature, here we argue that 'buffer capacity' should be used when referring to the ability to resist an external effect or disturbance without system collapse or significant changes in system functions and structure, e.g. a storm event that did not result in a large wind-throw. Buffer capacity may therefore be the synonym to 'ecological stability', originally defined in the 70's as the ability to resist changes from the outside (cf. Rutledge 1974, Rutledge et al. 1976). In contrast, 'adaptability', in our understanding, refers to the potential of a system to adapt to a disturbance or altered conditions without losing its integrity, e.g. a mixed-forests survives a bark-beetle infestation since only a few percent of the tree species in the stand are susceptible to the pest, the overall stand, however, continues to exist as a modified version of its previous self. However, buffer capacity and adaptability share that they are considered positive properties of an ecosystem.

In any case, the question remains how a greater buffer capacity or adaptive capacity of structurally complex forests may be explained. We hypothesize that in case of a forest, complex structures are usually related to the presence of many plant organs of different size, e.g. leaves, twigs, regeneration, dominant trees, intermediate trees and small trees in a given space. A large biomass is not necessarily related to a high complexity, since most biomass is stored in the stems, which contribute little to the stand level complexity. That is why previous research in primary forests around the world showed that the structural complexity and the basal area (as a proxy for biomass) of a forest, do not necessarily correlate (Ehbrecht et al. 2021). Also, biomass alone is not a satisfying proxy for the buffering or adaptive capacity of a forest. In contrast, it was shown that beside climatic changes high growing stock was an important factor when explaining the increased disturbances in forests (Seidl et al. 2011). While maximization of exergy storage might be achieved through ecosystem maturity (*sensu* Ludovisi 2014), it is important to consider that large biomass combined with low exergy storage was also described as an indication for a sub-optimal system (Jørgensen et al. 1995, Bendoricchio and Jørgensen 1997). Note that optimal in terms of maximizing exergy capture is not equivalent to the optimal in the sense of timber production where exergy is usually low since biomass is preferentially allocated to stemwood. Considering only the amount of biomass present in a forest is hence likely not a suitable measure to quantify the efficiency of the energy conversion in a forest system or its adaptive capacity.

For a high energetic efficiency, the amount of green (photosynthetically active material) is likely a better proxy than the wooden biomass stocked in the stand, since it is the leaves that capture the light, delivering exergy to the tree while woody biomass deals with the energy storage. Even for the quantification of energy storage it is unlikely that biomass alone is a good proxy, since wood-bound biomass does not contain particularly much exergy that could be used for adaptational processes. Wood rather stores anergy (energy not usable in the system; *sensu* Nielsen et al. 2020) that cannot be mobilized easily, unless decomposition takes over or the trees catch fire, releasing large amounts of energy in the form of heat, not usable by the tree itself. In contrast, fine roots, younger shoots, twigs and leaves possess a greater ability to respond to altered conditions or disturbances, for example by changing the growing direction or growing angle, halting or increasing lateral growth, etc. Leaves and fine roots can even respond by modifying the efficiency of resource use (Shipley and Meziane 2002). In addition, it is in the leaves where trees perform stress relief through enzymatic feedback systems when drought and high temperatures that result in oxidative stress, need to be compensated by an antioxidant system (Rennenberg et al. 2006) which requires exergy.

Significance of structural complexity

Against the background that future challenges due to climate change might result in a dramatically increased

importance of the buffer or adaptive capacity of an ecosystem, the above said has important implications. If it is possible to measure structural complexity of an ecosystem, one might be able to provide a proxy for its adaptive capacity. For trees and forests, the quantification of the overall structural complexity in three-dimensional (3D) space is today possible based on terrestrial, mobile and airborne 3D laser scanning (Atkins et al. 2018b, Ehbrecht et al. 2017; 2021, Seidel 2018, Dorji et al. 2021, Stiers et al. 2020, Willim et al. 2020). Global approaches based on spaceborne laser scanning from the international space station (ISS) by means of NASA's GEDI (global ecosystem dynamics investigation) also provide tools for an assessment of forest complexity and structure mapping (e.g. Schneider et al. 2020). With structure and complexity available, it is equally important to gain information on tree species identity. Here, large progress has also been made when it comes to species identification for example from infrared sensors (e.g. Pan et al. 2022). Silviculturists know ways to increase the complexity of managed forests (Peck et al. 2014), mimicking natural developments (e.g. Messier et al. 2013) or admixing additional tree species, resulting in forests that produce timber but that are almost as complex as primary forests at the same time (e.g. Stiers et al. 2020). Figure 1 provides a visual representation of the theoretical ideas present here.

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image1.emf available at <https://authorea.com/users/564504/articles/611290-towards-a-causal-understanding-of-the-relationship-between-structural-complexity-productivity-and-adaptability-of-forests-based-on-principles-of-thermodynamics>

Figure 1: Causal framework of the relationship between structural complexity, productivity and adaptability of forests

Conclusions

Here we argue that the consideration of thermodynamic theory in forest ecosystem research holds great potential for a meaningful interpretation of the effects of forest structural complexity. We propose that higher structural complexity positively relates to the photosynthetic capabilities of a forest, which relate to optimized thermodynamic processes and hence increased energy uptake, exergy storage and ultimately increased energy turnover and thus adaptability, two ultimate properties of evolutionary processes. More research is needed to empirically confirm that the hypothesized causal chain is true for forest ecosystems, consequently that structural complexity is a driver of a forest's ability to deal (buffer or adapt) with environmental stress. If so, management for complexity would be a reasonable option to increase the adaptability of forests to future challenges, particularly climate change, and it should be considered that such complex forest structures cannot be created overnight, meaning that management towards higher structural complexity is urgently needed.

Conflict of interest statement

The authors declare no conflict of interest.

Ethics statements

This work did not include any activities that might be unethical.

References

- Abel, D. L., & Trevors, J. T. (2006). Self-organization vs. self-ordering events in life-origin models. *Physics of Life Reviews*, 3 (4), 211-228.
- Ammer, C. (2021). Der Dauerwaldgedanke - Betrachtungen zu Alfred Möllers bekanntem Buch anlässlich der Neuauflage der vor 99 Jahren erschienenen Originalschrift. *Der Dauerwald* 64, 92-95
- Atkins, J. W., Fahey, R. T., Hardiman, B. S., & Gough, C. M. (2018a). Forest canopy structural complexity and light absorption relationships at the subcontinental scale. *Journal of Geophysical Research: Biogeosciences*, 123(4), 1387-1405.

- Atkins, J. W., Bohrer, G., Fahey, R. T., Hardiman, B. S., Morin, T. H., Stovall, A. E., ... & Gough, C. M. (2018b). Quantifying vegetation and canopy structural complexity from terrestrial LiDAR data using the `forestr` package. *Methods in Ecology and Evolution* , 9 (10), 2057-2066.
- Bendoricchio, G., & Jørgensen, S. E. (1997). Exergy as goal function of ecosystems dynamic. *Ecological modelling* , 102 (1), 5-15.
- Bolstad, P. V., Vose, J. M., & McNulty, S. G. (2001). Forest productivity, leaf area, and terrain in southern Appalachian deciduous forests. *Forest Science* , 47 (3), 419-427.
- Brillouin, L. (1960). Science and Information Theory. Academic Press: Cambridge, MA, USA, 1960.
- Binkley, D., Campoe, O. C., Gspaltl, M., & Forrester, D. I. (2013). Light absorption and use efficiency in forests: Why patterns differ for trees and stands. *Forest ecology and management* , 288 , 5-13.
- Camaretta, N., Ehbrecht, M., Seidel, D., Wenzel, A., Zuhdi, M., Merk, M. S., ... & Knohl, A. (2021). Using Airborne Laser Scanning to Characterize Land-Use Systems in a Tropical Landscape Based on Vegetation Structural Metrics. *Remote Sensing* , 13(23), 4794.
- Clausius, R. (1850). Über die bewegende Kraft der Wärme und die Gesetze, welche sich daraus für die Wärmelehre selbst ableiten lassen. *Annalen der Physik* . 79 (4): 368–397, 500–524.
- Clausius, R. (1854). Über eine veränderte Form des zweiten Hauptsatzes der mechanischen Wärmetheorie. *Annalen der Physik* . xciii (12): 481–506.
- D’Amato, A. W., Bradford, J. B., Fraver, S., and Palik, B. J. (2011). Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. *Forest Ecology and Management* , 262, 803–816. doi: 10.1016/j.foreco.2011.05.014
- Dorji, Y., Schuldt, B., Neudam, L., Dorji, R., Middleby, K., Isasa, E., ... & Seidel, D. (2021). Three-dimensional quantification of tree architecture from mobile laser scanning and geometry analysis. *Trees* , 35 (4), 1385-1398.
- Ehbrecht, M., Schall, P., Ammer, C., & Seidel, D. (2017). Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. *Agricultural and Forest Meteorology* , 242, 1-9.
- Ehbrecht, M., Schall, P., Ammer, C., Fischer, M., & Seidel, D. (2019). Effects of structural heterogeneity on the diurnal temperature range in temperate forest ecosystems. *Forest Ecology and Management* , 432 , 860-867.
- Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D. C., Puettmann, K. J., Nilus, R., Babweteera, F., Willim, K., Stiers, M., Soto, D., Boehmer, H. J., Burnett, M., Juday, G., Stephens, S. L. & Ammer, C. (2021). Global patterns and climatic controls of forest structural complexity. *Nature communications* , 12 (1), 1-12.
- Fonseca, J.C., Pardal, M.A., Azeiteiro, U.M., Marques, J.C. (2002). Estimation of ecological exergy using weighing parameters determined from DNA contents of organisms- A case study. *Hydrobiologia* , 475-476: 79-90.
- Forrester, D. I., Ammer, C., Annighöfer, P. J., Barbeito, I., Bielak, K., Bravo-Oviedo, A., ... & Pretzsch, H. (2018). Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests along a productivity and climate gradient through Europe. *Journal of Ecology* , 106 (2), 746-760.
- Gell-Mann, M., & Lloyd, S. (1996). Information measures, effective complexity, and total information. *Complexity* , 2 (1), 44-52.

- Gough, C.M., Atkins, J.W., Fahey, R.T., & Hardiman, B.S. (2019). High rates of primary production in structurally complex forests. *Ecology*, 100 (10) e02864.
- Harthun, M. (2017). Natürliche Walder: Unnötig, zu teuer, gefährlich, unmoralisch? Entwicklung natürlicher Walder in Hessen (III) – die Argumente der Kritiker. *Naturschutz und Landschaftsplanung* , 49 (6), S. 195–201.
- Heidenreich, M. G., & Seidel, D. (2022). Assessing Forest Vitality and Forest Structure Using 3D Data: A Case Study From the Hainich National Park, Germany. *Frontiers in Forests and Global Change* , 5 , 929106.
- Helliwell, D. R. (1997). Dauerwald. *Forestry: An International Journal of Forest Research* , 70 (4), 375-379.
- Holland, J. H. (1992). Complex adaptive systems. *Daedalus* ,121 (1), 17-30.
- Jorgensen, S.E., Mejer, H.F. (1981). Exergy as key function in ecological models. In Energy and Ecological Modelling. Developments in Environmental Modelling 1; Mitsch, W.J., Bosserman, R.W., Klopatek, J.M., Eds.; Elsevier: Amsterdam, The Netherlands, 1981; p. 839.
- Jorgensen, S.E (1990). Ecosystem theory, ecological buffer capacity, uncertainty and complexity. *Ecological Modelling* , 52: 125-133.
- Jorgensen, S.E (1992). Integration of Ecosystem Theories: A pattern. Dordrecht, The Netherlands.
- Jorgensen, S. E., Nielsen, S. N., & Mejer, H. (1995). Emergy, environ, exergy and ecological modelling. *Ecological modelling* ,77 (2-3), 99-109.
- Jorgensen, S.E (2002). Integration of Ecosystem Theories: A pattern. 3rd Edition. Dordrecht, The Netherlands.
- Juchheim, J., Ammer, C., Schall, P., & Seidel, D. (2017). Canopy space filling rather than conventional measures of structural diversity explains productivity of beech stands. *Forest Ecology and Management* , 395, 19-26.
- Knoke, T., and Seifert, T. (2008). Integrating selected ecological effects of mixed European beech–Norway spruce stands in bioeconomic modelling. *Ecological Modelling* , 210, 487–498. doi: 10.1016/j.ecolmodel.2007.08.011
- Kuuluvainen, T., Penttinen, A., Leinonen, K., & Nygren, M. (1996). Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: an example from boreal spruce forest in southern Finland. *Silva Fennica*, 30 (2-3): 315-328.
- Levin, S. (2003). Complex adaptive systems: exploring the known, the unknown and the unknowable. *Bulletin of the American mathematical Society* , 40 (1), 3-19.
- Lindenmayer, D. B., Margules, C. R., and Botkin, D. B. (2000). Indicators of Biodiversity for Ecologically Sustainable Forest Management. *Conservation Biology* , 14, 941–950. doi: 10.1046/j.1523-1739.2000.98533.x
- Lotka, A. J. (1922). Contribution to the energetics of evolution. *Proceedings of the National Academy of Sciences* , 8 (6), 147-151.
- Ludovisi, A. (2014). Effectiveness of entropy-based functions in the analysis of ecosystem state and development. *Ecological Indicators* , 36 , 617-623.
- Luvall J.C. and Holbo, H.R. (1989). Measurements of short term thermal responses of coniferous forest canopies using thermal scanner data. *Remote Sensing and the Environment* , 27, 1989, pages 1 - 10;
- Mejer, H.F.; Jorgensen, S.E. Exergy and ecological buffer capacity (1979). In Proceedings of the Conference on Ecological Modelling, Copenhagen, Denmark, 28 August–2 September 1979; pp. 829–846.
- Messier, C., Puettmann, K. J., & Coates, K. D. (Eds.). (2013). Managing forests as complex adaptive systems: building resilience to the challenge of global change. Routledge.

- Moller, A. (1922). Der Dauerwaldgedanke. Sein Sinn und seine Bedeutung. Reprint der Ausgabe von 1922, Verlag von Julius Springer gesetzt in eine moderne Schrift, Verlag Kessel: Remagen-Oberwinter
- Neill, A. R., and Puettmann, K. J. (2013). Managing for adaptive capacity: thinning improves food availability for wildlife and insect pollinators under climate change conditions. *Can. J. For. Res.* 43, 428–440. doi: 10.1139/cjfr-2012-0345.
- Nicolis, G., Prigogine, I. (1971). Fluctuations in nonequilibrium systems. *Proc. Natl. Acad. Sci.*, 68, 2102–2107.
- Nielsen, S.N., Muller, F., Marques, J.C., Bastianoni, S., Jorgensen, S.E. (2020). Thermodynamics in Ecology- An introductory review. *Entropy*, 22: 820.
- Odum, H.T, Pinkerton, R.C. (1955). Time’s speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *American Scientist* , 45: 331-343.
- Pan, X., Qiu, J., & Yang, Z. (2022). Identification of softwood species using convolutional neural networks and raw near-infrared spectroscopy. *Wood Material Science & Engineering* , 1-11.
- Peck, J. E., Zenner, E. K., Brang, P., & Zingg, A. (2014). Tree size distribution and abundance explain structural complexity differentially within stands of even-aged and uneven-aged structure types. *European journal of forest research* , 133 (2), 335-346.
- Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R. S., & Gessler, A. J. P. B. (2006). Physiological responses of forest trees to heat and drought. *Plant Biology* , 8 (05), 556-571.
- Rutledge, R.W. (1974). Ecological stability: a systems theory viewpoint. Oklahoma State University.
- Rutledge, R.W., Basore, B. L., & Mulholland, R. J. (1976). Ecological stability: an information theory viewpoint. *Journal of Theoretical Biology* , 57(2), 355-371.
- Schneider, E.D. and Kay, J. (1994): Complexity and thermodynamics. *Futures* , 26 (6): 626-647.
- Schneider, F. D., Ferraz, A., Hancock, S., Duncanson, L. I., Dubayah, R. O., Pavlick, R. P., & Schimel, D. S. (2020). Towards mapping the diversity of canopy structure from space with GEDI. *Environmental Research Letters* , 15 (11), 115006.
- Schrodinger, E. (1944). What Is Life; Cambridge University Press: Cambridge, UK, 1944.
- Seidel, D., Ehbrecht, M., & Puettmann, K. (2016). Assessing different components of three-dimensional forest structure with single-scan terrestrial laser scanning: A case study. *Forest Ecology and Management* , 381, 196-208.
- Seidel, D. (2018). A holistic approach to determine tree structural complexity based on laser scanning data and fractal analysis. *Ecology and Evolution* , 8 (1), 128-134.
- Seidel, D., Annighofer, P., Stiers, M., Zemp, C. D., Burkardt, K., Ehbrecht, M., ... & Ammer, C. (2019a). How a measure of tree structural complexity relates to architectural benefit-to-cost ratio, light availability, and growth of trees. *Ecology and Evolution* , 9 (12), 7134-7142.
- Seidel, D., Annighofer, P., Ehbrecht, M., Magdon, P., Wollauer, S., & Ammer, C. (2020). Deriving Stand Structural Complexity from Airborne Laser Scanning Data—What Does It Tell Us about a Forest? *Remote Sensing* , 12(11), 1854.
- Seidl, R., SCHELHAAS, M. J., & Lexer, M. J. (2011). Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biology* , 17 (9), 2842-2852.
- Shipley, B., & Meziane, D. (2002). The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Functional Ecology* , 16 (3), 326-331.

- Stiers, M., Willim, K., Seidel, D., Ehbrecht, M., Kabal, M., Ammer, C., & Annighofer, P. (2018). A quantitative comparison of the structural complexity of managed, lately unmanaged and primary European beech (*Fagus sylvatica* L.) forests. *Forest Ecology and Management* , 430, 357-365.
- Stiers, M., Annighofer, P., Seidel, D., Willim, K., Neudam, L., & Ammer, C. (2020). Quantifying the target state of forest stands managed with the continuous cover approach—revisiting Moller’s “Dauerwald” concept after 100 years. *Trees, Forests and People* , 1, 100004.
- Wang, D., Heckathorn, S. A., Barua, D., Joshi, P., Hamilton, E. W., & LaCroix, J. J. (2008). Effects of elevated CO₂ on the tolerance of photosynthesis to acute heat stress in C₃, C₄, and CAM species. *American Journal of Botany* , 95 (2), 165-176.
- Weigel, R., Bat-Enerel, B., Dulamsuren, C., Muffler, L., Weithmann, G., & Leuschner, C. (2022). Summer drought exposure, stand structure, and soil properties jointly control the growth of European beech along a steep precipitation gradient in northern Germany. *Global Change Biology* .
- Willim, K., Stiers, M., Annighofer, P., Ehbrecht, M., Ammer, C., & Seidel, D. (2020). Spatial patterns of structural complexity in differently managed and unmanaged beech-dominated forests in Central Europe. *Remote Sensing* , 12(12), 1907.