



**2 Forty milestones in landscape ecology: commemorating
3 the 40th anniversary of the Allerton Park workshop**

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10 Science advances nonlinearly, characterized by
 11 phases of rapid growth with breakthroughs and peri-
 12 ods of steady development with only incremental
 13 progress. Landscape ecology exemplifies this pat-
 14 tern: initially proposed as a distinct field 85 years ago,
 15 it developed steadily in Europe for about 40 years
 16 before experiencing swift global expansion in the
 17 1980s. Today, landscape ecology is a well-established
 18 field of study worldwide. One of the key catalysts
 19 for its burgeoning development in the 1980s was
 20 the Landscape Ecology Workshop held in Allerton
 21 Park, Illinois, USA, during April 25–27, 1983 (also
 22 known as the Allerton Park workshop). The work-
 23 shop has had profound influences on the develop-
 24 ment of landscape ecology by helping create a new
 25 paradigm centered on spatial heterogeneity, scale, and
 26 interdisciplinarity. The workshop report (Risser et al.
 27 1984) has been cited about 700 times as per Google
 28 Scholar. A discipline that fails to honor its past may
 29 diminish its capacity to envision the future. Thus,
 30 *Landscape Ecology*, the flagship journal of the Inter-
 31 national Association for Landscape Ecology (IALE),
 32 has published several invited articles to reflect on the
 33 significance of the workshop, both historically and in
 34 shaping future directions (Risser 1995; Wiens 2008;
 35 Risser and Iverson 2013; Wu 2013a; Foody 2023;
 36 Forman 2023; Frazier 2024; Pearson 2024). In cel-
 37 ebration of the 40th anniversary of the Allerton Park
 38 workshop, we have selected 40 key milestones and
 39 the 40 most cited articles to commemorate the endur-
 40 ing impact and legacy of this pivotal event.

41 Forty key milestones in landscape ecology

42 Defining and selecting key milestones

43 A milestone literally means “a milepost made of
 44 stone” or broadly “an important point in progress
 45 or development” (<https://www.merriam-webster.com/>). Here, we define milestones as groundbreaking or exceptionally influential events in the development of landscape ecology. These milestones can be either significant publications or historic meetings. For publications, we focus on new theories/perspectives, new methods/approaches, and exemplary case studies, all of which are directly related to the core topics of landscape ecology. To quantify “extraordinary influence”, we adopt the minimum number

of citations that a “citation classic” must have (i.e., 400), according to Eugene Garfield, the founder of ISI (now Clarivate Analytics) and a pioneer in bibliometrics and scientometrics (Garfield 1993). To put this in perspective, Van Noorden et al. (2014) showed that, based on Thomson Reuter’s Web of Science (now Clarivate Analytics, covering natural and social sciences as well as humanities), only about 0.026% of published articles from 1900 to 2014 had more than 1,000 citations. Based on the same database, Pendlebury (2020) reported that only 0.17% of the journal articles and proceedings papers between 1970 and 2020 were cited more than 500 times, and this percentage dropped precipitously to 0.04% for those cited more than 1,000 times. For meetings, we evaluate them more subjectively by examining whether they have substantially shaped the direction or increased the global influence of the field. Being the first meeting on a continent alone does not necessarily make it a milestone.

Based on the above criteria and after a painstaking process, we selected 40 milestones out of hundreds of candidates (Table 1). The selection process was difficult because of the subjectivity and ambiguity in the criteria. However, relying solely on metrics would not be accurate or fair. Although the milestones on the list are all important contributions to landscape ecology in certain ways, we acknowledge that our biases in academic training, research interests, and even cultural backgrounds certainly influenced the selection of these milestones. To provide a more comprehensive account of the field’s history, we supplement the primary list of 40 milestones with an additional set of 50 notable events (Table S1). In the following, we highlight some of the milestones, with comments on each milestone included in the tables.

The first 40 years of landscape ecology

Landscape ecology, coined by Carl Troll (1939), emerged as a regionally-focused research field that combined the pattern-oriented geographical approach, inspired by aerial photography, with the process-oriented functional approach embodied in the term “ecosystem” coined by Arthur Tansley (1935).¹ The term “biogeocenosis” was developed by the

¹ Although biogeochemistry is now considered a key component of ecosystem ecology, the term “biogeochemistry” had been coined by a Russian geochemist (Vernadsky 1926) nine years before the term “ecosystem” appeared for the first time.

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Table 1 Forty Milestones in landscape ecology

Chrono-logical Order	Time	Event	Notes on milestones	Google Scholar Cites (7/3/2023)
1	1939	Troll, C. 1939. Luftbildplan und ökologische Bodenforschung. Pages 241–298. Zeitschrift der Gesellschaft für Erdkunde, Berlin	Carl Troll (1939) coined the term, landscape ecology (landschaftsökologie), and defined it in 1968 as "the study of the main complex causal relationships between the life communities and their environment ... expressed regionally in a definite distribution pattern (landscape mosaic, landscape pattern) and in a natural regionalization at various orders of magnitude"	670 8.0
2	1947	Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1–22	Alex S. Watt (1947) conceptualized plant communities as dynamic patch mosaics, in which spatial pattern and ecological processes are related. This seminal paper has had far-reaching impacts in ecology, particularly in areas of disturbance ecology and patch dynamics	3410 44.9
3	1967	MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton	The MacArthur-Wilson theory was a primary inspiration for the initial development of the North American landscape ecology, and remains quite influential in modern landscape ecology, albeit often only heuristically. Metapopulation theory and patch dynamics are also conceptually linked to the theory of island biogeography	26,981 481.8
4	1967	Neeff, E. 1967. Die theoretischen Grundlagen der Landschaftslehre. Haack, Gotha, Germany	This German book has often been regarded as the first textbook on landscape ecology. The book has a geographical emphasis, with key terms such as geographical scale ranges, the smallest landscape ecological spatial units, and ecotope	489 8.7
5	1969	Levin, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240	Richard Levin (1969) developed the first metapopulation model (the Levin model or the patch-occupancy model). One year later he coined the term "metapopulation" and defined it as "a population of populations which go extinct locally and recolonize" in a book chapter, entitled "Some Mathematical Problems in Biology" (Levin 1970)	4,610 85.4
6	1974	Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation and community structure. Proceedings of the National Academy of Sciences (USA) 71:2744–2747	Simon A. Levin and Robert Paine (1974) developed the theory of patch dynamics, with a mathematical model that predicted the effects of disturbances on community structure, dynamics, and stability by relating landscape pattern to local population processes. An important follow-up study was published by the same authors was published seven years later, empirically demonstrating how the theory of patch dynamics can help understand community dynamics in a rapidly changing landscape (Paine and Levin 1981)	1254 25.6

Table 1 (continued)

Chrono-logical Order	Time	Event	Notes on milestones	Google Scholar Cites (7/3/2023)
7	1979	Bormann, F. H., and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem: Disturbance, Development and the Steady State Based on the Hubbard Brook Ecosystem Study. Springer-Verlag, New York	This book presented the shifting mosaic steady state model in detail to link the spatial pattern and ecosystem processes of a forested watershed. It was enormously influential in shaping the ecological thinking of forest ecosystems	4309 97.9
8	1981	The first international conference on landscape ecology	This conference held in the Netherlands was a watershed moment which brought together most of the pioneering landscape ecologists in Europe and North America for the first time. It was the beginning of the golden age of landscape ecology. The conference produced a proceedings which was published in the following year (Tallingii, S. P., and A. A. de Vree, eds. 1982. Perspectives in Landscape Ecology. Proceedings of the International Congress of the Netherlands Society of Landscape Ecology, Veldhoven, The Netherlands, April 6–11, 1981. Pudoc, Wageningen)	N/A
9	1981	Forman, R. T. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. <i>Bioscience</i> 31:733–740	Richard Forman and Michel Godron proposed the patch-corridor-matrix model as a new paradigm and a spatial language for contemporary landscape ecology. Two years before that, in the edited book, "Pine Barrens: Ecosystem and Landscape" (1979), Forman already proposed the landscape mosaic framework for studying population and ecosystem processes in heterogeneous landscapes composed of multiple ecosystems	1,409 33.5
10	1982	The establishment of the International Association for Landscape Ecology (IALE)	This historic event took place at the 6th International Symposium on Problems of Landscape Ecological Research, Pestany, Czechoslovak Socialist Republic (CSSR), October 29, 1982, hosted by Milan Ruzicka, a pioneering landscape ecologist in CSSR who served as Vice President of IALE and a member of the first editorial board of Landscape Ecology. Isaak S. Zonneveld from the Netherlands was elected the inaugural president	N/A

Table 1 (continued)

Chrono-logical Order	Time	Event	Notes on milestones	Google Scholar Cites (7/3/2023)
11	1983	The Allerton Park workshop on landscape ecology	This was the first landscape ecology meeting on the American continent, which was organized by Paul Risser, James Karr, and Richard Forman with support from NSF Ecology Program. It was participated by 25 people (23 from the US, one from Canada, and one from France). The workshop produced a report: Risser, P. G., J. R. Karr, and R. T. Forman. 1984. Landscape Ecology: Directions and Approaches. Illinois Natural History Survey Special Publ. 2, Champaign	703 17.6
12	1984	Naveh, Z., and A. S. Lieberman. 1984. Landscape Ecology: Theory and Application. Springer-Verlag, New York	This was the first English textbook on landscape ecology that had a global influence, emphasizing a holistic landscape ecology perspective based on the Total Human Ecosystem concept (THE). The key ideas of landscape as THE were presented two years before: Naveh Z (1982) Landscape ecology as an emerging branch of human ecosystem science. Advances in Ecological Research 12:189–237	2,588 66.4
13	1985	Pickett, S. T. A., and P. S. White, editors. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando	This edited book, with contributions from a number of leading ecologists, included both conceptual and empirical studies of disturbance ecology, patch dynamics, and nonequilibrium dynamics of ecosystems. It has been one of the most influential ecology books published since the 1980s	6,068 159.7
14	1986	Forman, R. T. T., and M. Godron. 1986. Landscape Ecology. Wiley, New York	This was the first landscape ecology textbook in North America, which has had a wide-spread impact on the development of the field around the world. It is a foundational book of landscape ecology based on the patch-based paradigm	7000 189.2
15	1986	The establishment of the US Chapter of IALE (US-IALE) and its first annual symposium	This groundbreaking event was held at University of Georgia, Athens, USA, January 15–17, 1986, and the symposium theme was “The Role of Landscape Heterogeneity in the Spread of Disturbance” (See Turner 2015 for details). US-IALE, which became the North American Regional Chapter of the International Association for Landscape Ecology (IALE-NA) in 2019, has been a primary leader in the development of modern landscape ecology since its birth	N/A

Table 1 (continued)

Chrono-logical Order	Time	Event	Notes on milestones	Google Scholar Cites (7/3/2023)
16	1986	O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton	This was one of the two books published in the 1980s that had profoundly influenced ecological thinking in the United States and much of the western world during the 1980s and 1990s (the other one being Allen and Starr 1982). It provides a lucid introduction to (ecological) hierarchy theory that explains why and how ecological systems are hierarchically organized based on process rates. Landscapes are explicitly discussed, which is one of the reasons why it has had a pervasive and lasting impact on the development of modern landscape ecology	3256 88.0
17	1987	The launching of the journal, Landscape Ecology	The founding of the flagship journal of IALE was one of the most important milestones in the history of landscape ecology. The founding Editor-in-Chief Frank Golley and 18 editorial board members were all eminent landscape ecologists as well as distinguished ecologists and geographers. They were from 10 countries (predominantly Europe and North America), including R. Forman, M. Gordon, W. Haber, S. Levin, Z. Nayeh, P. Risser, C. Steinitz, and I. Zonneveld	N/A
18	1987	Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. <i>Oikos</i> 49:340–346	This paper developed the concept of ecological neighborhood for scaling landscape heterogeneity based on organism movements in space and time. It has been a foundational paper for behavioral landscape ecology	996 27.7
19	1987	Gardner, R. H., B. T. Milne, M. G. Turner, and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. <i>Landscape Ecology</i> 1:19–28	This was the first paper that introduced percolation theory into landscape ecology as a neutral model framework for analyzing landscape pattern and predict phase transitions. Neutral landscape models have been widely used in theoretical and empirical studies during the past decades, significantly advancing our understanding of the processes and consequences of landscape fragmentation and connectivity	1,048 29.1
20	1988	O'Neill, R. V., J. R. Krummel, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelis, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. H. Dale, and R. L. Graham. 1988. Indices of landscape pattern. <i>Landscape Ecology</i> 1:153–162	This paper introduced three of the most commonly used landscape metrics (Dominance Index, Contagion Index, and Fractal Dimension), with application examples. It has been the most cited paper published in Landscape Ecology since 1987	2413 68.9

Table 1 (continued)

Chrono-logical Order	Time	Event	Notes on milestones	Google Scholar Cites (7/3/2023)
21	1989	Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. <i>Vegetatio</i> 80:107–138	This is one of the earliest and most influential papers that introduce spatial statistical methods into the analysis of (often autocorrelated) ecological and environmental data, including Moran's I, Mantel test, trend surface analysis, semi-variograms, and Kriging. A landmark book on spatial statistics for ecologists was published 16 years later: Fortin, M.-J., and M. R. T. Dale. 2005. <i>Spatial Analysis: A Guide for Ecologists</i> . Cambridge University Press, Cambridge (the 2nd edition was published in 2014)	3057 89.9
22	1989	Wiens, J. A. 1989. Spatial scaling in ecology. <i>Functional Ecology</i> 3:385–397	This has been one of the most influential papers on spatial scaling in ecology, articulating several key concepts and their relationships (e.g., grain, extent, scale domains, scale dependence, and scale discontinuity)	6,316 185.8
23	1989	Turner, M. G. 1989. Landscape ecology: The effect of pattern on process. <i>Annual Review of Ecology, Evolution, and Systematics</i> 20:171–197	This extremely influential review paper highlighted one of the most prominent themes of landscape ecology in North America—effects of spatial heterogeneity (often created by disturbances) on ecological processes	5,059 148.8
24	1991	Turner, M. G., and R. H. Gardner. 1991. Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag, New York	This was the first book devoted solely on quantitative methods in landscape ecology, focusing primarily on landscape pattern analysis and simulation modeling	1,544 48.3
25	1992	Levin, S. A. 1992. The problem of pattern and scale in ecology. <i>Ecology</i> 73:1943–1967	This has been the most influential paper on the issue of scale and scaling in ecology, which is a key research topic in modern landscape ecology.	9380 302.6
26	1994	Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscape with different proportions of suitable habitat: a review. <i>Oikos</i> 71:355–366	Habitat fragmentation implies a loss of habitat, reduced patch size and an increasing distance between patches, but also an increase of new habitat. In these landscapes, habitat fragmentation is primarily habitat loss. However, in landscapes with highly fragmented habitat, patch size and isolation will complement the effect of habitat loss and the loss of species or decline in population size will be greater than expected from habitat loss alone	4402 151.8
27	1995	Forman, R. T. T. 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge	This has been the most comprehensive and influential foundational book that presents the patch-based paradigm of modern landscape ecology	9162 327.2

Table 1 (continued)

Chrono-logical Order	Time	Event	Notes on milestones	Google Scholar Cites (7/3/2023)
28	1995	McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure. Gen. Tech. Rep. PNW-GTR-351. USDA Forest Service, Portland	This most widely used landscape pattern analysis software has greatly popularized the use of landscape metrics worldwide	5,393 192.6
29	1995	Riitters, K. H., R. V. O'Neil, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. A factor analysis of landscape pattern and structure metrics. <i>Landscape Ecology</i> 10:23–39	This paper provided the first comprehensive analysis of correlations and redundancy among landscape pattern metrics	1,829 65.3
30	1995	Wu, J., and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. <i>Quarterly Review of Biology</i> 70:439–466	This paper critiques the equilibrium paradigm in ecology and proposes a spatially explicit pattern-process-scale framework by integrating patch dynamics and hierarchy theory in a landscape context. It advocates that landscape ecology is not only a field of study, but also represents a new paradigm that applies to the science and practice of ecological systems across scales.	1725 61.6
31	1996	Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. <i>Landscape Ecology</i> 11:141–156	This was one of the early and most influential studies that examined how land use and land cover affected the biological integrity of streams on multiple spatial scales, using a landscape approach (with Habitat Index and Index of Biological Integrity). It has been one of the most cited papers in Landscape Ecology since 1987. Other influential papers on riverine landscape ecology include: Allan et al. 1997 (cited 1437 times), Ward et al. 2002 (cited 1390 times), Wiens 2002 (cited 1194 times), and Allan 2004 (cited 4532 times)	1152 42.7
32	2001	Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. <i>Landscape Ecology in Theory and Practice: Pattern and Process</i> . Springer-Verlag, New York	This has been one of the most influential landscape ecology textbooks for the past two decades, which focuses on the effects of landscape pattern on population processes, ecosystem dynamics, and spread of disturbances. The second edition was published in 2015	4,826 219.4
33	2002	Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter, editors. 2002. <i>Road Ecology: Science and Solutions</i> . Island Press, Washington, D.C	This was the first book on road ecology that emerged from landscape ecology but focused on the structure, function, and ecological influences of roads	3,278 156.1

Table 1 (continued)

Chrono-logical Order	Time	Event	Notes on milestones	Google Scholar Cites (7/3/2023)
34	2003	Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. <i>Annual Review of Ecology, Evolution, and Systematics</i> 34:487–515	This has been one of the most influential publications on habitat fragmentation and biodiversity, advocating that habitat loss and fragmentation per se must be explicitly distinguished in assessing their effects on biodiversity	9,919 496.0
35	2003	Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. <i>Trends in Ecology and Evolution</i> 18:189–197	This was the seminal paper that defined a new field of study: landscape genetics, which stimulated a flurry of research activities within landscape ecology and molecular ecology	2,961 148.1
36	2005	Antrop, M. 2005. Why landscapes of the past are important for the future. <i>Landscape and Urban Planning</i> 70:21–34	This influential paper analyzed the pattern and driving forces of European landscapes from a historical perspective, and discussed the importance of the diversity and identity of cultural landscapes	2,343 130.2
37	2008	Nassauer, J. I., and P. Ondra. 2008. Design in science: extending the landscape ecology paradigm. <i>Landscape Ecology</i> 23:633–644	This was a groundbreaking paper that proposed a pattern-process-design paradigm for landscape ecology	635 42.3
38	2009	Termorshuizen, J. W., and P. Ondra. 2009. Landscape services as a bridge between landscape ecology and sustainable development. <i>Landscape Ecology</i> 24:1037–1052	This was one of the earliest and most influential papers on landscape services, a concept that makes the ecosystem services concept more relevant to landscape planning/design and landscape sustainability	855 61.1
39	2011	Pijanowski, B., A. Farina, S. Gage, S. Dumyahn, and B. Krause. 2011. What is soundscape ecology? An introduction and overview of an emerging new science. <i>Landscape Ecology</i> 26:1213–1232	This is the first special issue on soundscape ecology that integrates the concepts and principles of landscape ecology with acoustic ecology, bioacoustics, and urban environmental acoustics	837 69.8
40	2013	Wu, J. 2013. Landscape sustainability science: ecosystem services and human well-being in changing landscapes. <i>Landscape Ecology</i> 28:999–1023	This paper coined the term, "landscape sustainability science", and defined what it is with a conceptual framework. This paper has become the second most cited paper published in <i>Landscape Ecology</i> since its inception in 1987. A sequel was published 8 years later: Wu, J. 2021. Landscape sustainability science (II): core questions and key approaches. <i>Landscape Ecology</i> 36:2453–2485	1,552 155.2

98 Russian geobotanist Vladimir N. Sukachev through a
 99 series of publications during the 1940s, and has often
 100 been regarded as equivalent to “ecosystem” (Dronin
 101 and Francis 2019). However, Troll (1971) consid-
 102 ered biogeocenosis to be “obviously identical with”
 103 landscape ecology. During the 1920s-1940s, multiple
 104 efforts led by prominent geophysical and biological
 105 scientists in Europe and the former USSR aimed to
 106 achieve a similar goal: understanding and managing
 107 the landscape in its totality by integrating the living
 108 organisms with their geophysical environment—the
 109 agglomeration of botany, zoology, hydrology, pedol-
 110 ogy, geomorphology, geochemistry, meteorology, cli-
 111 matology, silviculture, and land management.

112 In 1968, Troll defined landscape ecology as “the
 113 study of the main complex causal relationships
 114 between the life communities and their environment
 115 expressed regionally in a definite distribution
 116 pattern (landscape mosaic, landscape pattern)” (Troll
 117 1971). This initial definition of landscape ecology
 118 clearly resembled Tansley’s (1935) definition of eco-
 119 system. However, the emphasis in Troll’s definition
 120 on the regionally expressed landscape mosaic of mul-
 121 tiple ecosystems gave landscape ecology a distinctive
 122 feature. In 1967, the German geographer Ernst Neef,
 123 who is sometimes considered a founder of landscape
 124 ecology along with Carl Troll, published the first text-
 125 book on landscape ecology (Neef 1967). The book
 126 (in German) had a geographical emphasis, with key
 127 terms such as geographical scale ranges, the small-
 128 est landscape ecological spatial units, and ecotope.
 129 Interestingly, the classic paper on plant communities
 130 as patch mosaics by Alex S. Watt (1947), which had
 131 a profound influence on patch dynamics and distur-
 132 bance ecology in North America during the 1970s
 133 and 1980s, had no detectable impact on the early
 134 development of landscape ecology in Europe.

135 For the first 40 years, the development of land-
 136 scape ecology took place primarily in Germany, the
 137 rest of Central Europe, and the former USSR, with
 138 related but distinct efforts led by prominent geogra-
 139 phers and ecologists. A substantial amount of pio-
 140 neering interdisciplinary landscape (and geoecologi-
 141 cal) research was accomplished during this period,
 142 which has been well documented in several reviews
 143 (e.g., Naveh 1982; Bastian and Steinhardt 2002;
 144 Dronin and Francis 2019; Frolova 2019). Landscape
 145 ecology not only originated in Europe, but also devel-
 146 oped a strong interdisciplinary vision in its early

decades, integrating biology, ecology, geography, 147
 land appraisal/management, and landscape planning/ 148
 design holistically in a regionally expressed land- 149
 scape mosaic. This salient theme of early European 150
 landscape ecological studies—often described as 151
 being “transdisciplinary” and “holistic”—seems more 152
 relevant today than ever, as sustainability is the great- 153
 est challenge of our time. 154

However, for some 40 years since Troll (1939), 155
 the field developed rather slowly, and the research 156
 activities were confined mainly to Central Europe. 157
 One motivation for the Allerton Park workshop was 158
 the observation that the field was going through “a 159
 conceptual bottleneck” with multiple definitions and 160
 ideas that had “never been coalesced, organized, 161
 and confronted rigorously to produce a theoreti- 162
 cally sound basis for understanding landscape-scale 163
 interactions” (Risser et al. 1984). The workshop was 164
 intended to help advance the field by exploring and 165
 identifying a coherent set of relevant theories, ques- 166
 tions, and approaches. 167

The golden age of landscape ecology 168

The period from the 1980s to the 1990s marked the 169
 golden age of landscape ecology. During the late 170
 1970s and early 1980s, a new and different version 171
 of landscape ecology was developed independently 172
 in North America, characterized by the patch-cor- 173
 ridor-matrix (PCM) model (Forman 1979, 1981, 174
 1983; Forman and Godron 1981, 1986). The PCM 175
 model focuses on the structure, function, and dynam- 176
 ics of landscape elements (i.e., patches, corridors, 177
 and matrix), and provides a “spatial language” for 178
 ecologists, geographers, and managers/planners to 179
 communicate and collaborate. The first internation- 180
 al conference on landscape ecology, held in the Nether- 181
 lands in 1981, provided the first ever opportunity for 182
 European and North American landscape ecologists 183
 to exchange their ideas in person (Forman 2015). In 184
 1982, the International Association for Landscape 185
 Ecology (IALE) was established through a joint effort 186
 by landscape ecologists from both sides of the North 187
 Atlantic. 188

While Carl Troll (1939), inspired by aerial photog- 189
 raphy and the concept of ecosystem, merged geog- 190
 raphy and ecology to give rise to landscape ecology, 191
 MacArthur and Wilson (1967), in their search for the 192
 underlying processes of the species-area relationship, 193

integrated ecology with geography to develop the theory of island biogeography (IBT). With pervasive influences on biogeography, ecology, and evolutionary biology in general (Losos and Ricklefs 2010; Whittaker et al. 2017), the IBT played an instrumental role in shaping the conceptual foundation of landscape ecology in North America. Several key models and theories, such as the PCM model, metapopulation theory (Levins 1969, 1970), and patch dynamics (Levin and Paine 1974; Pickett and White 1985), were inspired by and conceptually related to the IBT. Spatial patchiness in terrestrial landscapes is ubiquitous, often created and maintained by natural and anthropogenic disturbances that lead to nonequilibrium ecological dynamics. This “patchiness-disturbance” perspective, often traced back to the early work of Watt (1947) on vegetation mosaic, became increasingly dominant in ecological thinking in North America in the 1970s and 1980s (Levin and Paine 1974; Whittaker and Levin 1977; Pickett and Thompson 1978; Paine and Levin 1981; Pickett and White 1985).

The 1983 Allerton Park workshop, the first meeting on landscape ecology in North America, brought together the previously mentioned concepts, theories, and methods, and explicitly established spatial heterogeneity as the central theme of landscape ecology, catalyzing a surge of studies on the pattern-process-scale relations. The core questions proposed at the workshop have stimulated and shaped the development of landscape ecology worldwide ever since, and they remain relevant today (Turner et al. 2001; Wiens 2008; Wu 2017; With 2019; Forman 2023; Pearson 2024). The establishment of the US Chapter of IALE (US-IALE; now IALE-NA) and its inaugural symposium in 1986 marked a watershed moment, ushering in a new and transformative era for landscape ecology. A year later, the flagship journal of IALE, *Landscape Ecology*, was launched, which played a critical role in publishing some of the most original and creative ideas in landscape ecology (see Barrett et al. 2015; Wu 2017). With these developments, new kinds of landscape ecologists joined the field, with interests in population ecology, behavioral ecology, and disturbance ecology in heterogeneous landscapes.

New ideas, theories, and quantitative methods proliferated from the late 1980s through the 1990s, significantly advancing and reshaping the field during this dynamic period. Concepts like spatial heterogeneity, pattern analysis, disturbance, patch dynamics,

pattern-process relationships, scale, hierarchy, neutral landscape models, fractals, and habitat fragmentation soon became buzzwords in landscape ecology (e.g., Gardner et al. 1987; Turner 1987; Turner and Gardner 1991; Forman 1995a, b; Wu and Loucks 1995; Farina 1998). All of these topics were centered on spatial heterogeneity—its causes, processes, and consequences. The interplay between pattern, process, and scale quickly emerged as the dominant paradigm, shaping the trajectory of the field. The rapid development of landscape ecology was also boosted by the availability of remote sensing data, computers, and GIS (Iverson et al. 1989; Haines-Young et al. 1993; Iverson 2007; Foody 2023). The launch of the Landsat satellite in 1972, along with other technological breakthroughs in remote sensing, GIS, and GPS, revolutionized geographic and environmental sciences and played a pivotal role in advancing landscape ecology during this time period. These technological advances allowed for the rapid development of landscape metrics and other spatial analysis/modelling methods (O'Neill et al. 1988; Legendre and Fortin 1989; Turner and Gardner 1991; McGarigal and Marks 1995; Gustafson 1998), which were a key characteristic of modern landscape ecology.

Two seminal books on hierarchy theory—Allen and Starr (1982) and O'Neill et al. (1986)—had a major influence on the development of landscape ecology during the 1980s and 1990s, particularly in advancing the understanding of spatial scaling of landscape patterns and processes. Several seminal papers on scale and scaling by landscape ecologists followed, with pervasive influences across ecology, geography, and other related fields (e.g., Delcourt and Delcourt 1988; Turner et al. 1989; Wiens 1989; Levin 1992). By integrating hierarchy theory and patch dynamics through a multiscale, spatially explicit framework, the hierarchical patch dynamics paradigm (Wu and Loucks 1995) links several ecological theories together, including Watt's (1947) early conceptualization of plant communities as patch mosaics, patch dynamics (Levin and Paine 1974; Pickett and White 1985; Wu and Levin 1994), the shifting mosaic steady state model (Bormann and Likens 1979), and land mosaics (Forman 1995a). Landscape ecology also became “wetter” by focusing more on “waterscapes”. The emergence of riverscape ecology, in particular, revolutionized traditional approaches to studying rivers by emphasizing the importance of spatial

292 heterogeneity and connectivity in rivers and their
 293 surrounding landscapes (Roth et al. 1996; Allan et al.
 294 1997; Ward et al. 2002; Allan 2004). The landmark
 295 publication “Land Mosaics: The Ecology of Land-
 296 scapes and Regions” by Forman (1995a) remains the
 297 most-cited book in landscape ecology.

298 This golden era was a time of rejuvenation and
 299 revolution (in the sense of a paradigm shift), which
 300 resulted in what can be called, “modern” or “con-
 301 temporary” landscape ecology. This updated and
 302 expanded version of landscape ecology had a stronger
 303 ecological foundation, and helped to free landscape
 304 ecology from the confines of being perceived solely
 305 as an “applied science” by many earlier landscape
 306 ecologists. It opened up new opportunities for theo-
 307 retical and experimental explorations of the causes,
 308 processes, and consequences of spatial heterogeneity.
 309 Within a decade, landscape ecology found its way to
 310 Australia, China, and other parts of the world (Lud-
 311 wig et al. 1997; Cao et al. 2002; Fu and Lü 2006). By
 312 the 1990s, landscape ecology emerged as one of the
 313 most exciting and dynamic disciplines in both ecol-
 314 ogy and geography in North America and Europe. It
 315 emerged as a leading field in spatial pattern analysis
 316 and scaling within and beyond ecological and geo-
 317 graphical sciences (Gibson et al. 1998; Wu et al.
 318 2006; Frazier et al. 2023).

319 A pluralistic field both diversifying and converging

320 Since the beginning of the twenty-first century, land-
 321 scape ecology has continued to strengthen its sci-
 322 entific foundation that hinges on the relationship
 323 between spatial heterogeneity and ecological pro-
 324 cesses. Modern landscape ecology is not just a field
 325 of study; it also represents a new ecological-geosocial
 326 paradigm that views the world through a multiscale
 327 pattern-process lens. A number of new research
 328 frameworks and directions have emerged, delving
 329 into specific landscape types and thematic issues.
 330 Textbooks and monographs have mushroomed, each
 331 recognizing spatial heterogeneity as a central theme,
 332 but offering distinct perspectives on the scope and
 333 main topics of the field (e.g., Farina 1998, 2022;
 334 Turner et al. 2001; Burel and Baudry 2003; Wiens
 335 and Moss 2005; Wu and Hobbs 2007; Turner and
 336 Gardner 2015; With 2019). With its historical roots in
 337 geography, ecology, and other disciplines, landscape
 338 ecology has always been inherently interdisciplinary

and pluralistic. Therefore, the concurrent trends of
 339 diversification and convergence within the field are
 340 not surprising, nor do they signal an “identity cri-
 341 sis”. This dual process is a characteristic of a rapidly
 343 evolving interdisciplinary field, where diverse per-
 344 spectives enhance understanding while convergence
 345 fosters coherence and actionable insights.

346 Interfacing with other well-established disciplines,
 347 landscape ecology has several new subfields that are
 348 still rapidly developing. Urban landscape ecology has
 349 been one of the most active area of research across
 350 ecological and geographical sciences in recent dec-
 351 ades (Jenerette and Wu 2001; Luck and Wu 2002;
 352 Jenerette et al. 2007; Buyantuyev et al. 2010; Fernan-
 353 dez and Wu 2016; Muderere et al. 2018). Road ecol-
 354 ogy emerged in the early 2000s (Forman et al. 2002),
 355 focusing on the ecological impacts of roads and
 356 transportation networks—particularly on issues such
 357 as roadkill, habitat fragmentation, and species inva-
 358 sions. Landscape ecology’s principles, such as patch-
 359 corridor-matrix model and landscape connectivity,
 360 are foundational to road ecology. Landscape genetics
 361 integrates landscape ecology principles with popula-
 362 tion genetics, focusing on the effects of landscape het-
 363 erogeneity on genetic flows and biodiversity (Manel
 364 et al. 2003). This integration has allowed for a more
 365 nuanced understanding of how spatial patterns affect
 366 species survival and adaptation in fragmented land-
 367 scapes. Related to metapopulations and patch dynam-
 368 ics, the concepts of meta-communities (Leibold et al.
 369 2004) and meta-ecosystems (Loreau et al. 2003) were
 370 developed, aiming to understand how spatial hetero-
 371 geneity affects community organization and ecosys-
 372 tem processes. Combining principles of bioacoustics
 373 and landscape ecology led to the development of
 374 soundscape ecology which aims to understand how
 375 the landscape of biological, geophysical, and anthro-
 376 pogenic sounds—the soundscape—influence and are
 377 influenced by the communication, behavior, and dis-
 378 tribution of species, as well as how soundscape pat-
 379 tern reflects the function and health of ecosystems
 380 (Pijanowski et al. 2011).

381 Landscape epidemiology, as a concept first pub-
 382 lished by the Russian parasitologist Evgeny N. Pav-
 383 lovsky (1966), reemerged as a vibrant field of study
 384 in the 2000s as a result of the interactions between
 385 landscape ecology and (spatial) epidemiology, both
 386 of which were boosted by GIS, remote sensing, and
 387 advanced spatial analysis methods (Kitron 1998;

388 Ostfeld et al. 2005). This revitalized field focuses
 389 on the impacts of landscape and environmental heterogeneity, including land-use changes, habitat alterations, and climate variability, on the distribution and
 390 dynamics of vector-borne diseases. This interdisciplinary approach helps in predicting disease outbreaks
 391 and designing effective intervention strategies by explicitly recognizing the critical role of landscape
 392 structure in shaping ecological interactions that influence health outcomes. In addition, “seascape ecology” has become firmly established, which combines
 393 marine science and landscape ecology to understand the causes and ecological consequences of spatial patterning in seas and oceans (Pittman et al. 2011, Pittman 2018). Conceptually, this line of research can
 394 trace back to, among others, the earlier marine studies of patch dynamics (e.g., Levin 1978; Steele 1978,
 395 1989).

406 Since the early 2000s, landscape ecology has
 407 become increasingly integrative and holistic, evidenced by the surge of interests in highly inter- and
 408 transdisciplinary topics. For example, landscape ecological principles and methods have been increasingly
 409 integrated in landscape design/planning to create
 410 more resilient and sustainable landscapes (Botequilha
 411 Leitao and Ahern 2002; Nassauer and Opdam 2008;
 412 Ahern 2013; Hersperger et al. 2021). Several influential publications have emphasized the importance of
 413 historical landscape changes and driving forces for
 414 understanding and planning sustainable landscapes
 415 (Bürgi et al. 2004; Antrop 2005; Milovanovic et al.
 416 2020). Studies of landscape effects on ecosystem
 417 services have mushroomed in recent decades, leading
 418 to the emergence of the “landscape services”
 419 concept, which emphasizes the services provided by
 420 both individual ecosystems and their interactions in a
 421 landscape (Termorshuizen and Opdam 2009; Turner
 422 et al. 2013; Bastian et al. 2014; Bürgi et al. 2015;
 423 Plieninger et al. 2019). Landscape services is “an
 424 extremely apt bridging concept that links landscape
 425 pattern, ecosystem services, aesthetics, values, and
 426 decision making” (Wu 2013b), which is also closely
 427 related to landscape multifunctionality (Lovell and
 428 Taylor 2013; Mastrangelo et al. 2014; Sturck and
 429 Verburg 2017; Lavorel et al. 2022), landscape resilience
 430 (Cumming 2011; Cumming et al. 2013; Arnaiz-Schmitz
 431 et al. 2023), and landscape sustainability
 432 (Potschin and Haines-Young 2006, 2013; Wu 2006,
 433 2013b, 2021; Naveh 2007; Musacchio 2009, 2013;

434 Opdam et al. 2018). Landscape multifunctionality is
 435 a necessary but insufficient condition for both landscape
 436 resilience and sustainability; similarly, landscape
 437 resilience is essential for sustainability but does
 438 not guarantee it (Wu 2021).

439 In the past two decades, landscape ecology has
 440 also expanded rapidly around the world, evidenced
 441 by several impactful international events and by the
 442 changing landscape of scientific publications in the
 443 field (see the next section). Since its establishment in
 444 1982, IALE has held 11 world congresses (once every
 445 four years). Five took place in Europe: Roskilde,
 446 Denmark in 1983; Münster, Germany in 1987; Toulouse,
 447 France in 1995; Wageningen, the Netherlands
 448 in 2007; and Milan, Italy in 2019. Three were held
 449 in North America: Ottawa, Canada in 1991; Snowmass,
 450 Colorado, USA in 1999; and Portland, Oregon,
 451 USA in 2007. Thus, eight out of the 11 world con-
 452 gresses have been held in Europe and North Amer-
 453 ica. The other three were held in Darwin, Australia
 454 in 2003 (the 6th); Beijing, China in 2011 (the 8th);
 455 and Nairobi, Kenya in 2023 (the 11th), respectively.
 456 The 12th is scheduled to take place in Valparaiso,
 457 Chile in 2027 (the first in South America). These
 458 events clearly demonstrate that landscape ecology has
 459 become a truly global science. As the field expands
 460 scientifically and geographically, landscape ecology
 461 is becoming more prominent in addressing global
 462 issues, including biodiversity conservation, climate
 463 change mitigation and adaptation, and many of the
 464 17 Sustainable Development Goals (Wu 2017, 2021;
 465 Gilman and Wu 2023; Frazier 2024). These recent
 466 developments highlight the growing influences of
 467 landscape ecology and its role in shaping sustainable
 468 landscapes across diverse regions worldwide.

471 Forty most-cited papers in landscape ecology

472 Landscape ecological studies have proliferated since
 473 the onset of the golden era in the early 1980s. Based
 474 on the Web of Science (WoS) database, Wu (2017)
 475 reported that the number of articles published in
 476 *Landscape Ecology* and the number of articles contain-
 477 ing the terms “landscape” and “ecolog*” in their
 478 titles, abstracts, or keywords across all other outlets
 479 combined, both increased exponentially from 1987
 480 to 2016. Using a more extensive database, Scopus,
 481

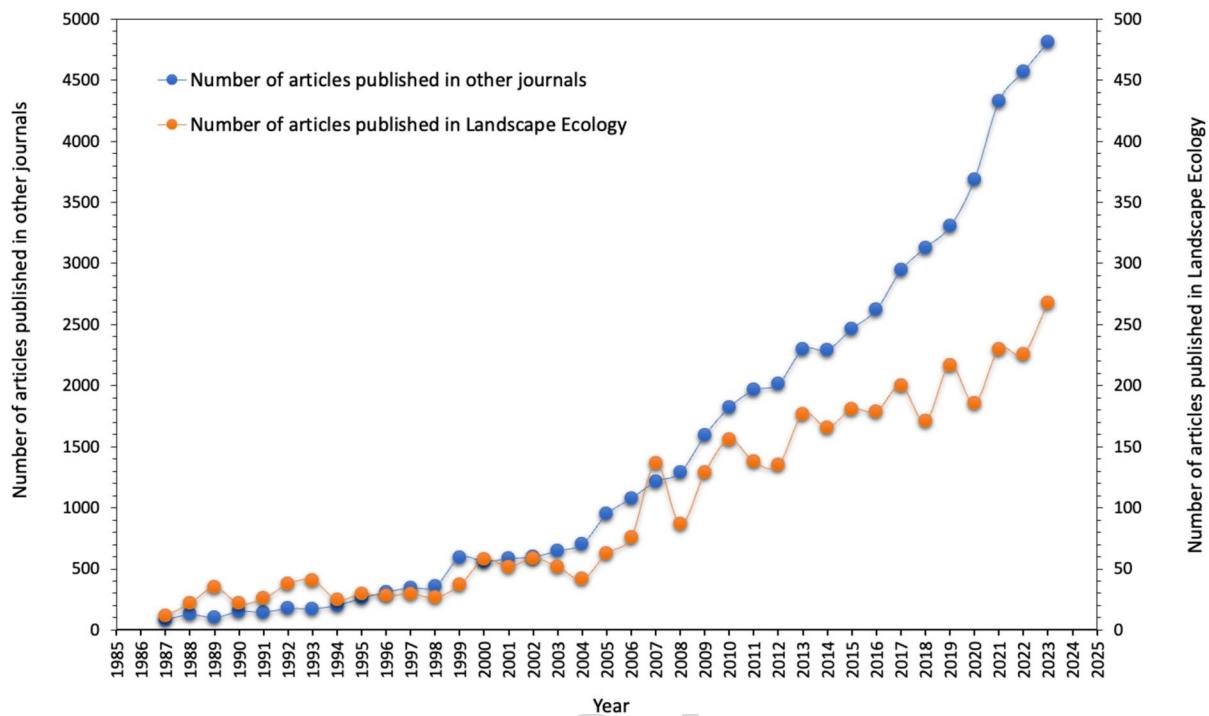


Fig. 1 The number of articles published in the journal, *Landscape Ecology* (in red) and the number of landscape ecology-relevant articles published in other journals (i.e., those whose

titles, abstracts, or keywords contained the words “landscape” and “ecolog*”), based on Scopus (<https://www.scopus.com>; accessed in June 2024)

we show here that this increasing trend has continued beyond 2016, with articles from all other sources exhibiting an even faster acceleration rate (Fig. 1). The top 10 countries with the most publications between 1987 and 2023 are: USA, China, UK, Australia, Canada, Germany, France, Spain, Brazil, and Italy (Fig. 2). USA has been the largest contributor to the literature in landscape ecology, leading China by a ratio of 2.3 to 1 in total contributions. However, China's annual output became the second highest around 2005, soared rapidly since then, and nearly caught up with the US by 2023 (Fig. 2). For articles published in *Landscape Ecology*, the dominance of the US is even more apparent, and the major contributing countries are similar to those across all other publication outlets, though in a slightly different order (Fig. 3). Given the history of modern landscape ecology discussed above, this is somewhat expected.

Landscape ecological research has increasingly been published in a variety of well-established mainstream journals associated with professional societies. However, in recent years, a number of journals

from publishers like MDPI and PLOS, which pour out thousands of articles per year per journal, have further boosted the number of landscape ecology-related articles. The current scientific publishing landscape is unprecedentedly muddy and chaotic.² The flagship journal of a scientific society, by definition, is the most reliable barometer of a discipline's development. So, here we list the top 40 most cited papers from the IALE's flagship journal—*Landscape Ecology* from 1987 to 2023 (Table 2). Previously, Wu (2013a) reported the top 20 most cited papers during 1987–2012, and Wu (2017) listed the top 30 most cited papers during 1987–2016. Comparing this top 40 list with the other two lists can help us better understand the dynamics of the most appealing topics and the most influential papers in this field since the Allerton Park workshop.

² A recent report by the InterAcademy Partnership (2022) discussed some widespread concerns with scientific publishing today and recommended a series of measures to address mal-practices (<https://www.interacademies.org/publication/predatory-practices-report-English>).

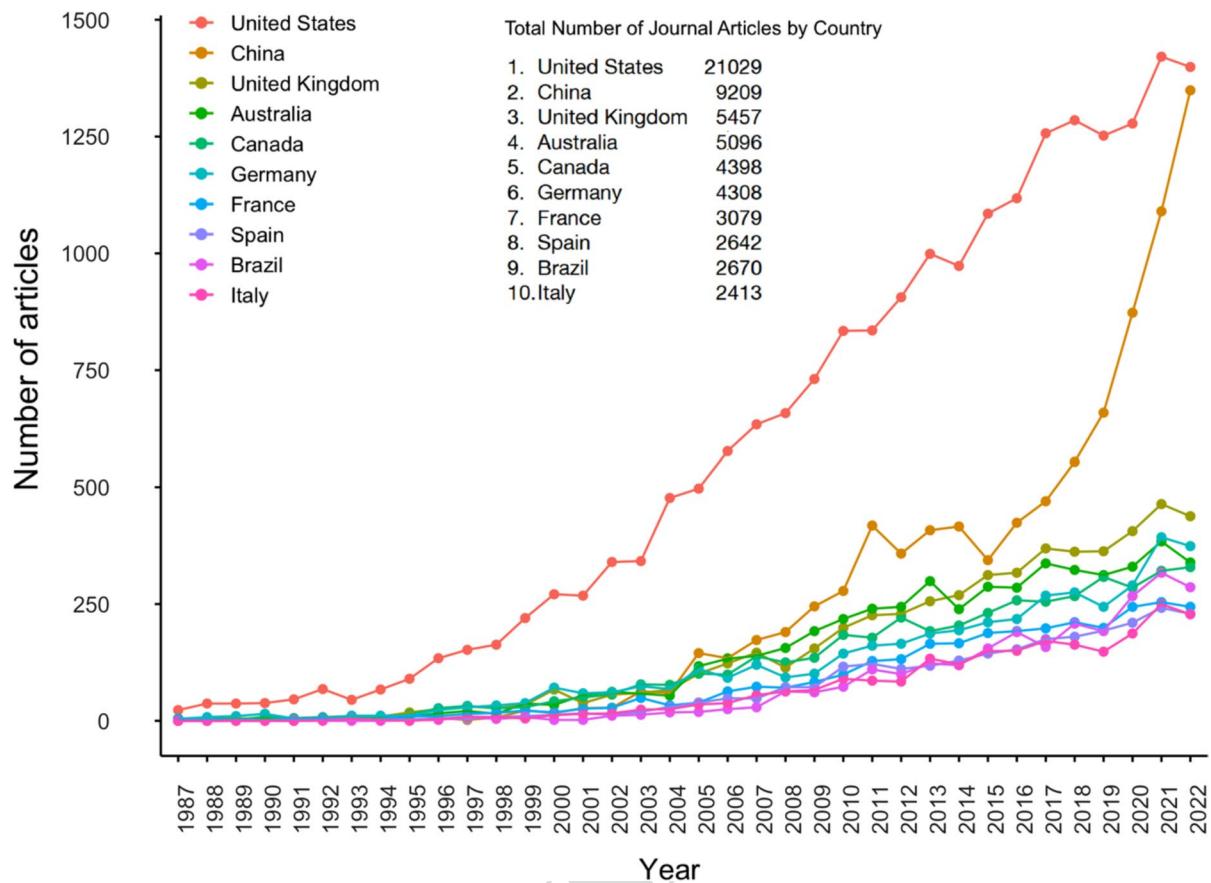


Fig. 2 Top 10 countries with most published landscape ecology-related articles (as per author affiliations) during 1987–2022 based on Scopus (<https://www.scopus.com>; accessed in

June 2023). Landscape ecology-relevant articles refer to those that contained both the words “landscape” and “ecolog*” in their titles, abstract, or keywords

Fig. 3 Top 30 countries that had the most articles published in the journal, *Landscape Ecology*, between 2002 and 2022, based on Scopus (<https://www.scopus.com>; accessed in June 2023)

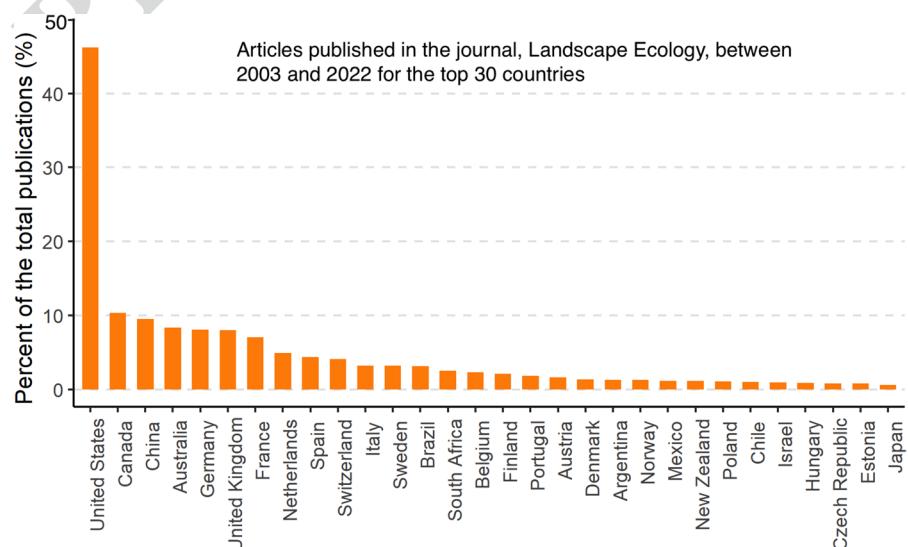


Table 2 The forty most-cited articles published in Landscape Ecology, the flagship journal of the International Association for Landscape Ecology (IALE), based on data from Scopus (<https://www.scopus.com>; accessed on June 22, 2024)

Authors	Year	Article title	# Cites
O'Neill R.; Krummel J.; Gardner R.; Sugihara G.; Jackson B.; DeAngelis D.; Milne B.; Turner M.; Zygmunt B.; Christensen S.; Dale V.; Graham R	1988	Indices of landscape pattern	1271
Wu J	2013	Landscape sustainability science: Ecosystem services and human well-being in changing landscapes	1033
Riitters K.; O'Neill R.; Hunsaker C.; Wickham J.; Yankee D.; Timmins S.; Jones K.; Jackson B	1995	A factor analysis of landscape pattern and structure metrics	1007
Wu J	2004	Effects of changing scale on landscape pattern analysis: Scaling relations	906
Luck M.; Wu J	2002	A gradient analysis of urban landscape pattern: A case study from the Phoenix metropolitan region, Arizona, USA	802
Turner M.; O'Neill R.; Gardner R.; Milne B	1989	Effects of changing spatial scale on the analysis of landscape pattern	796
Jaeger J.A.G	2000	Landscape division, splitting index, and effective mesh size: New measures of landscape fragmentation	772
Mitsch W.; Bernal B.; Nahlik A.; Mander Ü.; Zhang L.; Anderson C.; Jørgensen S.; Brix H	2013	Wetlands, carbon, and climate change	751
Zeller K.; McGarigal K.; Whiteley A	2012	Estimating landscape resistance to movement: A review	720
Gobster P.; Nassauer J.; Daniel T.; Fry G	2007	The shared landscape: What does aesthetics have to do with ecology?	718
Forman R.T.T	1995	Some general principles of landscape and regional ecology	708
Li H.; Wu J	2004	Use and misuse of landscape indices	662
Roth N.E.; David Allan J.; Erickson D.L	1996	Landscape influences on stream biotic integrity assessed at multiple spatial scales	652
Pascual-Hortal L.; Saura S	2006	Comparison and development of new graph-based landscape connectivity indices: Towards the prioritization of habitat patches and corridors for conservation	650
Wu J.; Hobbs R	2002	Key issues and research priorities in landscape ecology: An idiosyncratic synthesis	645
Bürgi M.; Hersperger A.; Schneeberger N	2005	Driving forces of landscape change—Current and new directions	636
Buyantuyev A.; Wu J	2010	Urban heat islands and landscape heterogeneity: Linking spatiotemporal variations in surface temperatures to land-cover and socioeconomic patterns	634
Matthews R.; Gilbert N.; Roach A.; Polhill J.; Gotts N	2007	Agent-based land-use models: A review of applications	633
Franklin J.F.; Forman R.T.T	1987	Creating landscape patterns by forest cutting: Ecological consequences and principles	632
Verburg P.H.; Overmars K.P	2009	Combining top-down and bottom-up dynamics in land use modeling: Exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model	629
Jelinski D.E.; Wu J	1996	The modifiable areal unit problem and implications for landscape ecology	614
Falcucci A.; Maiorano L.; Boitani L	2007	Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation	601
Seto K.C.; Fragkias M	2005	Quantifying spatiotemporal patterns of urban land-use change in four cities of China with time series landscape metrics	573

Table 2 (continued)

Authors	Year	Article title	# Cites
Gardner R.; Milne B.; Turnei M.G.; O'Neill R	1987	Neutral models for the analysis of broad-scale landscape pattern	559
Hargis C.D.; Bissonette J.A.; David J.L	1998	The behavior of landscape metrics commonly used in the study of habitat fragmentation	521
Turner M.G	1990	Spatial and temporal analysis of landscape patterns	503
Termorshuizen J.W.; Opdam P	2009	Landscape services as a bridge between landscape ecology and sustainable development	482
Lovell S.T.; Taylor J.R	2013	Supplying urban ecosystem services through multifunctional green infrastructure in the United States	477
Wu J.; Shen W.; Sun W.; Tueller P.T	2002	Empirical patterns of the effects of changing scale on landscape metrics	469
Pijanowski B.; Farina A.; Gage S.; Dumyahn S.; Krause B	2011	What is soundscape ecology? An introduction and overview of an emerging new science	468
Turner M.G.; Romme W.H	1994	Landscape dynamics in crown fire ecosystems	461
Van Oost K.; Govers G.; Desmet P	2000	Evaluating the effects of changes in landscape structure on soil erosion by water and tillage	455
Baguette M.; Van Dyck H	2007	Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal	441
Ahern J	2013	Urban landscape sustainability and resilience: The promise and challenges of integrating ecology with urban planning and design	439
Connors J.P.; Galletti C.S.; Chow W.T.L	2013	Landscape configuration and urban heat island effects: Assessing the relationship between landscape characteristics and land surface temperature in Phoenix, Arizona	438
Vogt P.; Riitters K.H.; Estreguil C.; Kozak J.; Wade T.G.; Wickham J.D	2007	Mapping spatial patterns with morphological image processing	428
Plotnick R.E.; Gardner R.H.; O'Neill R.V	1993	Lacunarity indices as measures of landscape texture	420
McGarigal K.; Wan H.; Zeller K.; Timm B.; Cushman S	2016	Multi-scale habitat selection modeling: a review and outlook	407
Gustafson E.J.; Parker G.R	1992	Relationships between landcover proportion and indices of landscape spatial pattern	404
Kindlmann P.; Burel F	2008	Connectivity measures: A review	402

521 The list of top 40 most cited papers published in
 522 *Landscape Ecology* between 1987 and 2023 reveals
 523 several important trends and insights. Together,
 524 they reflect both some of the enduring core research
 525 themes and emerging key topics of modern landscape
 526 ecology (Forman 1995b; Wu and Hobbs 2002). First,
 527 several central themes have continued to attract much
 528 attention, such as landscape metrics (e.g., O'Neill
 529 et al. 1988; Gustafson and Parker 1992; Plotnick et al.
 530 1993; Riitters et al. 1995; Li and Wu 2004), scale
 531 effects and scaling (e.g., Turner et al. 1989; Jelinski
 532 and Wu 1996; Wu et al. 2002; Wu 2004; McGarigal
 533 et al. 2016), fire disturbance (e.g., Turner and Romme
 534 1994), and landscape connectivity and habitat frag-
 535 mentation (Hargis et al. 1998; Jaeger 2000; Baguette

and Van Dyck 2007; Kindlmann and Burel 2008; Zeller et al. 2012). This is not surprising because spatial heterogeneity is the cornerstone of modern landscape ecology. Heterogeneity begets patterns. Studying the ecology of landscapes requires quantifying heterogeneity through pattern analysis. Patterns affect processes, both of which are scale-dependent. As a result, scale effects occur, and scaling becomes necessary for understanding and predicting across landscapes. Fire disturbance and habitat fragmentation (or connectivity) are quintessential “landscape” phenomena that effectively illustrate how spatial patterns, ecological processes, and scale interact, thus consistently receiving substantial attention from landscape ecologists.

551 The list also highlights several emerging areas
552 from recent decades. Research on urban landscapes
553 has been growing more rapidly in both quantity and
554 diversity than other types of landscapes, such as agri-
555 cultural lands and natural areas. As a pluralistic sci-
556 ence, landscape ecology has continued to integrate
557 with other disciplines, creating new research fron-
558 tiers in response to global environmental challenges.
559 Specifically, the emerging areas include the quantifi-
560 cation of the spatiotemporal patterns of urbanization
561 (Luck and Wu 2002; Seto and Fragkias 2005), urban
562 heat islands (Buyantuyev and Wu 2010; Connors
563 et al. 2013), landscape services (Termorshuizen and
564 Opdam 2009), landscape genetics (Zeller et al. 2012),
565 soundscape ecology (Pijanowski et al. 2011), climate
566 change mitigation (Connors et al. 2013; Mitsch et al.
567 2013), urban ecosystem services and green infrastruc-
568 ture planning (Ahern 2013; Lovell and Taylor 2013),
569 and, currently a major focus, landscape sustainabil-
570 ity and resilience (Cumming 2011; Ahern 2013; Wu
571 2013b). During the past two decades, the field has
572 increasingly emphasized broadly interdisciplinary
573 and transdisciplinary subjects, such as urban ecology,
574 climate change, and landscape sustainability, which
575 links landscape pattern, biodiversity, ecosystem func-
576 tion, ecosystem services, human wellbeing, and land-
577 scape planning and governance. This is not surpris-
578 ing, as landscape sustainability should be the ultimate
579 goal of landscape ecological studies. Overall, the list
580 of the forty most-cited papers in *Landscape Ecology*
581 generally supports our selection of the forty mile-
582 stones in the field presented above.

583 Concluding remarks

584 The Allerton Park workshop has played a pivotal role
585 in advancing landscape ecology by introducing a new
586 paradigm (Wiens 2008; Wu 2013a; Forman 2023;
587 Pearson 2024). This paradigm integrates several eco-
588 logical and geographical theories and perspectives—
589 such as patch dynamics, disturbance ecology, island
590 biogeography theory, landscape geography, and pop-
591 ulation and ecosystem ecology—to study the ecol-
592 ogy of spatial heterogeneity, which remains a central
593 theme in landscape ecology today. It also underscored
594 the importance of spatial pattern analysis and mod-
595 eling, particularly through remote sensing, GIS, and
596 potentially AI-driven methods for pattern recognition

and classification (Risser et al. 1984). Indeed, remote
597 sensing and GIS are now indispensable tools for land-
598 scape ecologists, and AI and big data seem poised to
599 transform landscape ecology and other related sci-
600 ences in years to come (Hampton et al. 2013; Runtu
601 et al. 2020).

We observe that the significance of the Allerton
603 Park workshop is not universally recognized. For
604 example, several recent reviews of landscape ecol-
605 ogy history by European authors do not even men-
606 tion it (e.g., Bastian and Steinhardt 2002; Francis and
607 Antrop 2021; Van Eetvelde and Aagaard Christensen
608 2023). On the other hand, early European contribu-
609 tions have often been underrepresented in publica-
610 tions by authors outside Europe. From the 40 mile-
611 stones and most-cited papers presented here on this
612 special occasion, it is evident that landscape ecology
613 originated in Europe as a hybrid between geography
614 and ecology in the 1930s. It developed slowly as a
615 localized research area for about four decades, but
616 with a strong holistic and geographic character.

The field burst into bloom globally in the 1980s
618 and 1990s. During this golden era, geographically
619 differentiated ideas began to coalesce, galvanized
620 by new ecological theories, analytical methods, and
621 digital technologies. As a result, landscape ecology
622 became a globally recognized discipline. However,
623 nothing grows forever. Since the turn of the century,
624 landscape ecology has entered a phase of steady
625 development. Interestingly, but not surprisingly, the
626 transdisciplinarity and holistic thinking that char-
627 acterized landscape ecology in its early stages have
628 once again become central themes of the field today,
629 with a more urgent and challenging goal—to main-
630 tain and design sustainable landscapes in the Anthro-
631 pocene. This trend seems inevitable because sustain-
632 ability has become the theme of our time, and because
633 global sustainability cannot be achieved without first
634 sustaining our landscapes.

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