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Mechanical ecology – taking biomechanics to the field

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Abstract

Interdisciplinary research can have strong and surprising synergistic effects, leading to rapid knowledge gains. Equally important, it can help to reintegrate fragmented fields across increasingly isolated specialist sub-disciplines. However, the lack of a common identifier for research ‘in between fields' can make it difficult to find relevant research outputs, and network effectively. We illustrate and address this issue for the emerging interdisciplinary hotspot of 'mechanical ecology', which we define here as the intersection of quantitative biomechanics and field ecology at the organism level. We show that an integrative approach crucially advances our understanding in both disciplines by (1) putting biomechanical mechanisms into a biologically meaningful ecological context and (2) addressing the largely neglected influence of mechanical factors in organismal and behavioural ecology. We call for the foundation of knowledge exchange platforms such as meeting symposia, special issues in journals, and focus groups dedicated to mechanical ecology.

Introduction

The twenty-first century has seen interdisciplinary research rise to unprecedented popularity (Van Noorden 2015), with new research fields emerging at the intersection of historically well separated academic areas. Biomimetics (Bhushan 2009) – the application of biological principles to engineering design – and structural biology (Banaszak 2000, Gu & Bourne 2009) – the combination of molecular biology, biochemistry and physics – are examples of disciplines born from the novel combination of methods, expertise and ideas. The challenges that come with cross-disciplinary collaboration are frequently outweighed by synergistic effects resulting in true quantum leaps of knowledge gain. Examples are the fusion of computer science and molecular biology into bioinformatics (Pevsner 2015), or the application of engineering methods such as finite element analysis to solve biomechanical and evolutionary questions (Rayfield 2007). A similar need for 're-integration' exists even within the field of biology, which has split up into a myriad of subdisciplines, often based on organisational level and methodology (e.g. Gunton *et al.* 2019, reintegratingbiology.org). Here, we illustrate this for the emerging indisciplinary field of 'mechanical ecology', which we define as the combination of biomechanics and field ecology at the organism level (Figure 1).

The concept of linking biomechanics and ecology is not new (Herrel *et al.* 2006) – the great Steven Vogel did that in essence, albeit not explicitly, in his wonderful books 'Life's Devices' (Vogel 1988) and 'Comparative Biomechanics: Life's Physical World' (Vogel 2013). Anthony Herrel, Thomas Speck and Nick Rowe (2006) explicitly noted that a focus on – often neglected – (bio-)mechanical factors can provide outstanding answers to ecological questions when they published an early synopsis of the young field. In the U.S., Mark Denny and colleagues quickly realized the potential of applying the insights gained from field biomechanics (i.e. mechanical ecology) to explain and predict large-scale ecological processes at the population and ecosystem level, and coined the term 'ecomechanics' for this approach (Denny & Helmuth 2009; Denny & Gaylord 2010). Despite the publication of a dedicated textbook (Denny 2016), the use of the term 'ecomechanics' remained largely restricted to the U.S. science community and has been mainly applied in a marine ecology context. One could argue that it is the research that matters more than the terminology applied to define it; however, clear and intuitive keywords help to find research outputs as well as people with similar research interests. We would therefore like to encourage to use the terms 'ecomechanics' and 'mechanical ecology' widely to identify interdisciplinary studies combining biomechanics and ecology. For the sake of clarity, we suggest applying the term 'ecomechanics' to the study of large-scale, population- to ecosystem-level phaenomena and use 'mechanical ecology' for studies concerned with the individual organism and its functioning and survival in an ecologically meaningful context (Figure 1). In that sense, mechanical ecology directly complements ecophysiology, chemical and behavioural ecology – all mainly focused on interactions at the organism level. By putting biomechanical form-structure-function relationships into ecological context, mechanical ecology offers a meaningful interpretation of the *biological relevance* of those mechanisms, and provides the foundation for the higher-level ecomechanical analyses and models. In other words, mechanical ecology takes biomechanics out of the laboratory and into the field.

Linking biomechanics and ecology adds significant value to both

Both ecomechanics and mechanical ecology provide crucial links between two established and important, yet surprisingly poorly connected research fields. Biomechanics traditionally focused on animals and humans. As such, it can often be equated with functional morphology and concentrates on locomotion, stability and biomaterials, commonly in a sports or medical context (Knudson 2007, Fung 2013a, b). Even where questions go beyond this limited scope, most studies are laboratory-based. They tackle proximate, mechanistic questions with quantitative experiments or theoretical models, but frequently fail to test their findings in a meaningful ecological context. Ecology, on the other hand, still largely neglects mechanical factors when it comes to explaining interactions at the organism level, and instead focuses on physiology, biochemistry and behaviour. Controlled experimental approaches are often hindered by the complexity of field conditions and the limited availability of replicates. As a result, ecological research has repeatedly been criticized for relying too much on counting and correlating, and sometimes even violating good statistical practice in the process (Scheiner & Gurevitch 2001, Møller & Jennions 2002).

The study of plant-animal interactions traditionally revolves around chemical ecology (Schoonhoven *et al.* 2006). Nowadays we know that many other factors and signals play a role: optical (McCrea & Levy 1983, Whitney *et al.* 2009, Jacobs *et al.* 2016, Fritz *et al.* 2017), tactile/vibrational (Kevan & Lane 1985, Cocroft 2001), structural/mechanical (Griffiths 2006, Whitney & Federle 2013) and even electrical (Clarke *et al.* 2013, 2017). In addition, organisms face physical challenges in their environment just as much as chemical and physiological ones: anchoring in unstable environments (Abelson & Denny 1997, Koehl 1999, Stokes 2002, Méndez-Alonzo *et al.* 2015), withstanding physical impacts and stresses (Boulding 1984, Niklas 1999, Vincent & Wegst 2004, Fournier *et al.* 2013), and moving safely and efficiently in physically diverse environments (Peattie 2009, Wu 2011, Forterre 2013, McGowan & Collins 2018). The need to integrate biomechanical research into the ecological context – and, vice versa, to investigate ecological questions within a physical-biomechanical framework – has been noted repeatedly (Harmer *et al.* 2010, Combes *et al.* 2012, Whitney & Federle 2013, Vallejo-Marín 2019, Killen *et al.* 2017, Russell *et al.* 2019). Especially in a physical/mechanical context, plants and animals often face similar challenges, and find surprisingly similar solutions (Lentink *et al.* 2009, Gorb *et al.* 2019). At a time when animal and plant science are increasingly separated – evidenced by the existence of separate departments for both at many universities – mechanical ecology can help to reconnect these major disciplines. Indeed, one might want to include microbiology as well here, since micro-organisms also face similar physical challenges. The convergent evolution of splash cups for spore or seed dispersal, respectively, in Nidulariaceae fungi (Martin 1927, Hassett *et al.* 2013) and *Chrysosplenium* sp. and *Mazus* sp. flowering plants (Amador *et al.* 2013) strikingly illustrates how similar mechanical principles are utilized to the same end across natural kingdoms.

A short history of mechanical ecology: challenges and advances

The transfer of experimental methods and approaches from the lab to the field is far from easy, and for many years, the combined investigation of ecology and biomechanics was largely confined to theoretical modelling and meta-analyses of the existing literature (e.g. Rowe & Speck 2005, Hein *et al.* 2011, Ditsche & Summers 2014). From force measurement setups to wind tunnels or rheometers, much of the typical biomechanics toolkit is bulky, heavy, and far from weatherproof. Therefore it does not come as a surprise that the first generation of biomechanical field equipment was custom-built by the researchers themselves. Supplying power is an additional problem in remote field locations. Remarkably, some of the earliest successful attempts to overcome the limitations of quantitative field measurements were made by marine biologists who may well face the harshest of all research environments (e.g. LaBarbera & Vogel 1976, Carrington Bell & Denny 1994). It is fair to say that the emerging field of mechanical ecology was pioneered by marine and benthic researchers (Denny *et al.* 1985, Denny 1987, Koehl 1999).

Early studies of terrestrial mechanical ecology often used methodology from ecological research to collect data in the field, and then analysed and interpreted the results in a biomechanical context. Bruderer *et al.* (1995) used radar tracking to measure the altitude and flight speed of migrating birds and analysed the results in the context of meteorological measurements, concluding that altitude choice was driven by a single variable, tail wind speed. Hedenström *et al.* (2002) used the same method to measure airspeed and altitude of arctic birds and used the data to test predictions from flight mechanical theory. Around the same time, others started to combine data from laboratory and field experiments in order to gain new insights. Federle *et al.* (1997) used running trials under different experimental conditions in the field to test the ability of 23 ant species to walk on the slippery stems of *Macaranga* ant-plants. Having thus identified 11 species of interest, they then used a centrifuge to measure friction forces of those ants on Perspex surfaces in the lab (Federle *et al.* 2000). The surprising result – high-performing species from the field did worst in the friction tests – is a striking reminder why it is so important to verify biomechanical findings from the lab under natural conditions in the field. Many other studies have since shown similar performance gaps between lab and field measurements (Combes *et al.* 2012, Astley *et al.* 2013).

Over the following decade, more and more scientists started to take biomechanics to the field. Widely used biomechanical methods such as force measurements were adapted for field use, often with highly creative approaches. Anderson *et al.* (2006) used a spring tensiometer to measure the forces required to dislodge sediment-growing tropical green algae in the natural habitat on the Panama coast. Bohn (2007) used a modified bending beam strain gauge setup to measure buoyancy forces of submerged ants in a field laboratory in Borneo. Endlein *et al.* (2013) measured attachment forces of torrent frogs in a field station in the middle of the Bornean rainforest. Their simple portable setup consisted of a motor-controlled rotating platform attached to a flow-controlled running water system to simulate natural conditions on rocks in fast-flowing streams. Moen *et al.* (2013) used a similar setup, as well as high-speed video recordings, to collect field data on the attachment ability, jumping and swimming performance of frogs from three continents for a large-scale comparative analysis. Stark & Yanoviak (2018) investigated adhesion and locomotion of arboreal ants on different dry and wet surfaces in a field laboratory on Barro Colorado Island, Panama (see also Stark *et al.* 2018). Friction and adhesion forces were measured by pulling manually on a handheld spring scale that was attached to the ant via a thin string. Higham *et al.* (2017a) used a portable load cell to record forelimb friction forces and body masses of arboreal geckos in the field in French Guiana. These and further morphometric data from literature then informed a model to calculate the forces that the animals experience when landing on leaves after performing escape jumps from the canopy.

Locomotion has always been at the centre of animal biomechanics. Yanoviak *et al.* (2005) studied the kinematics and ecology of controlled voluntary jump-gliding descents of tropical canopy ants in Panama. Bohn *et al.* (2012) performed 3D kinematic analyses of swimming ants filmed with two synchronised high speed cameras in the field in Borneo. Thompson *et al.* (2018a,b) developed a much larger scale portable 3D kinematics setup to study the locomotion of wild mountain gorillas (*Gorilla beringei beringei*) in the field. Higham *et al.* (2017b) took this even further and captured the 3D kinematics of rattlesnake strikes during natural hunting forays at night, using infrared-sensitive highspeed cameras. The study of locomotion in naturally behaving wild animals not only greatly improved our understanding of the complex interplay of mechanical factors and ecology, but also sparked some rather remarkable discoveries along the way. While observing the unique swimming behaviour of pitcher plant-inhabiting *Colobopsis schmitzi* ants in Borneo, Bohn & Federle (2004) coincidentally discovered a previously unknown trapping mechanisms in these carnivorous plants. The trapping function of the collar-like pitcher rim, a striking wetness-activated 'aquaplaning' mechanism, had been overlooked in over a century of carnivorous plant research, probably due to its reliance on environmental wetness. Bauer *et al.* (2008) later took a custom-built conductance measurement setup to the tropical field sites to continuously monitor surface wetness on pitcher traps, identify natural sources of wetness, and show that capture rates in the field were directly proportional to the amount of wetting.

Plant biomechanics also moved out to the field. The main questions revolved around the multitude of plant growth forms and the resulting form-structure-function relationships. Which trade-offs exist between growth forms, and why do some plants change their growth form during ontogeny

(Gallenmüller *et al*. 2001, 2004; Isnard *et al.* 2005)? Field studies often used relatively simple mechanical rigs such as three-point bending frames or spring-loaded cylinders to measure the material properties of stems and branches. More recently, Clair *et al.* (2019) and Lehnebach *et al.* (2020) used portable biaxial strain gauges connected to a data logger to directly measure strain release in the bark of trees growing in a tilted position in the field. In combination with lab investigations of bark microstructure, the results elucidated how the development of asymmetric stresses in the bark helps trees to maintain or regain an upright posture under constant or repeated loading. The importance of such field-based research for the plant biomechanics community is reflected in special sessions like 'Ecological and evolutionary biomechanics' at the triennial Plant Biomechanics Conference.

Maximal biological relevance, or maximal measurement accuracy – what to prioritize?

Do we really need to do all measurements *in situ*, in a fully natural setting? From the examples above it becomes apparent that there may be a trade-off between measurement accuracy on one hand and ecological relevance of the experiments on the other hand. In order to be portable, field setups are usually simplified and rely less on mains-powered devices. For example, motor-controlled stages in friction force measurements are commonly replaced by (less reproducible) manual pulling. On the other hand, the sacrifice in measurement accuracy may be outweighed by the advantages of using freshly collected animals, plants or material specimens for the experiments, because these are more likely to behave naturally (e.g. Djawdan & Garland 1988, Edelmann *et al.* 2005, Klocke & Schmitz 2011). Ultimately, researchers will have to decide on a case-by-case basis whether to conduct a measurement in the lab, in a simplified field laboratory, or *in situ* in the natural habitat, and a combination of all three, in conjunction with theoretical calculations and modelling, is likely to be the most powerful approach. The technological limitations are continually diminishing as the increasing popularity of field biomechanics drives the development of ever more lightweight, portable equipment. Inspired by the work of Gaume & Forterre (2007) on the viscoelastic trap fluid of tropical *Nepenthes* pitcher plants, Collett *et al.* (2015) developed a portable extensional rheometer that matched the performance of standard laboratory instruments at a fraction of the size, weight and costs.

The increasing commercial availability of lighter, smaller, easier-to-use and more affordable devices is likely to boost biomechanical field research in the next decade. Recent advances in remote sensing technology such as the miniaturisation of sensors and power supplies, especially when combined with machine vision and machine learning algorithms, are opening up new avenues to collect field data (Jeanniard-du-Dot *et al.* 2016, Thompson *et al.* 2018a,b, Hubel *et al.* 2016, Liu *et al.* 2019). Modern high-speed cameras can be as small as a cubic inch, and models the size of a commercial DSLR offer impressive specs. Especially when combined with other technologies such as accelerometers, inertial measurement units and GPS trackers, animal-mounted micro-cameras can provide fascinating new insights into animal locomotion and behaviour (Wilson *et al.* 2013, Patel *et al.* 2017). Micro-computers such as the Arduino and Raspberry-Pi offer unprecedented possibilities for the development of custom instruments and automated data collection (Kwok 2017, Pasquali *et al.* 2017). The opportunities to take biomechanics out to the field – or in other words, the times for mechanical ecology research – have certainly never been better than now.

Conclusions and outlook

In summary, it is absolutely essential that we put insights gained in the lab to the test in the field. Only by taking an integrative approach, we can fully unravel biomechanical mechanisms without neglecting relevant environmental factors. We have seen in the example from the Federle lab that lab and field experiments can produce highly contradictory results (Federle *et al.* 1997, Federle *et al.* 2000), and taking only one side into account can lead to misinterpretations. The growing awareness of the importance of integrative approaches (Harmer *et al.* 2010, Combes *et al.* 2012, Whitney & Federle 2013, Killen *et al.* 2017, Moore & Biewener 2017, Vallejo-Marín 2019, Russell e*t al.* 2019) and steady increase of publications of biomechanical field studies (Figure 2) provide clear evidence that the field is moving in the right direction. The increasing availability of affordable lightweight yet powerful instruments and devices for field work will almost certainly accelerate this trend further.

When writing this review, it became quickly apparent that relevant publications, despite being plentiful, were frustratingly difficult to find. Despite the increased popularity of the field on both sides of the Atlantic Ocean, a *Scopus* search for publications with both 'biomechanics' and 'ecology' in the keywords in late 2019 returned no more than 288 hits (Table1). Even though nearly two thirds of those are from the most recent decade (Figure 2), testifying to the fast growth of the field, the total number is tiny compared to over 200,000 hits for 'ecology' on its own, and nearly as many for 'biomechanics'. Combination of search keywords such as 'biomechanics AND field' or previously established terms such as 'ecomechanics' also returned only a few relevant articles. In most cases, we had to combine these search terms with specific topic areas (e.g. 'migration', 'adhesion') in order to increase the relevance of the results. In other cases, we searched for specific authors – obviously only an option for a user who is already somewhat familiar with the field. This shows that there are still severe barriers to knowledge exchange hindering the progression of the field.

Van Noorden (2015) showed that interdisciplinary research papers are initially slow to pick up citations, even though they often outperform single-discipline papers in the longer term. By defining mechanical ecology in direct analogy to chemical and behavioural ecology – also largely field-based and focused at the organism level – we attempt to provide a more intuitive keyword that will help to find relevant research. We are aware that this is only a small first step and ultimately, it will be crucial to establish networking platforms dedicated to mechanical ecology. First steps towards this aim can be symposia at broad interdisciplinary conferences – SICB and SEB being obvious choices – and special journal issues devoted to mechanical ecology. When placed carefully in widely read ecology or plant-animal interaction journals, these could promote mechanical ecology to a broad scientific audience. In the long term, we hope to see a Society or Division for Mechanical Ecology established to raise the profile of the discipline, bring like-minded researchers together and foster knowledge exchange, collaboration and innovation.

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Author contributions

UB conceived the paper, compiled and analysed data, and wrote the initial draft. All authors wrote the final manuscript together.

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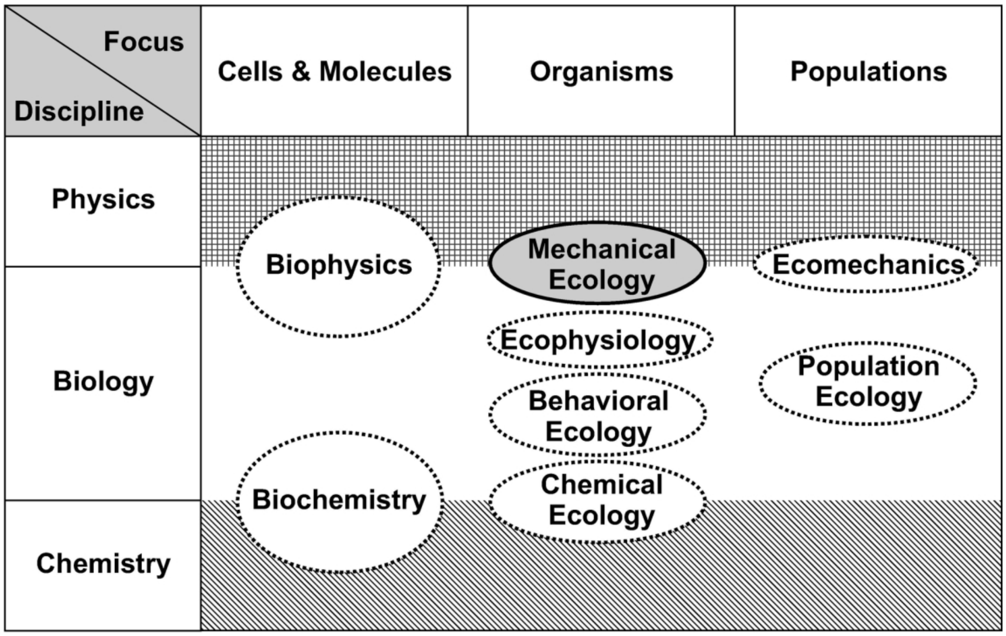

Figure 1. Schematic overview of the scientific ‘niche’ that the field of Mechanical Ecology occupies. On an axis from small- to large-scale phaenomena, it complements Biophysics and Ecomechanics, each at the intersection of physics and biology. On an organism-level scale, it directly complements the biological disciplines of Ecophysiology and Behavioral Ecology, and the interdisciplinary field of Chemical Ecology.

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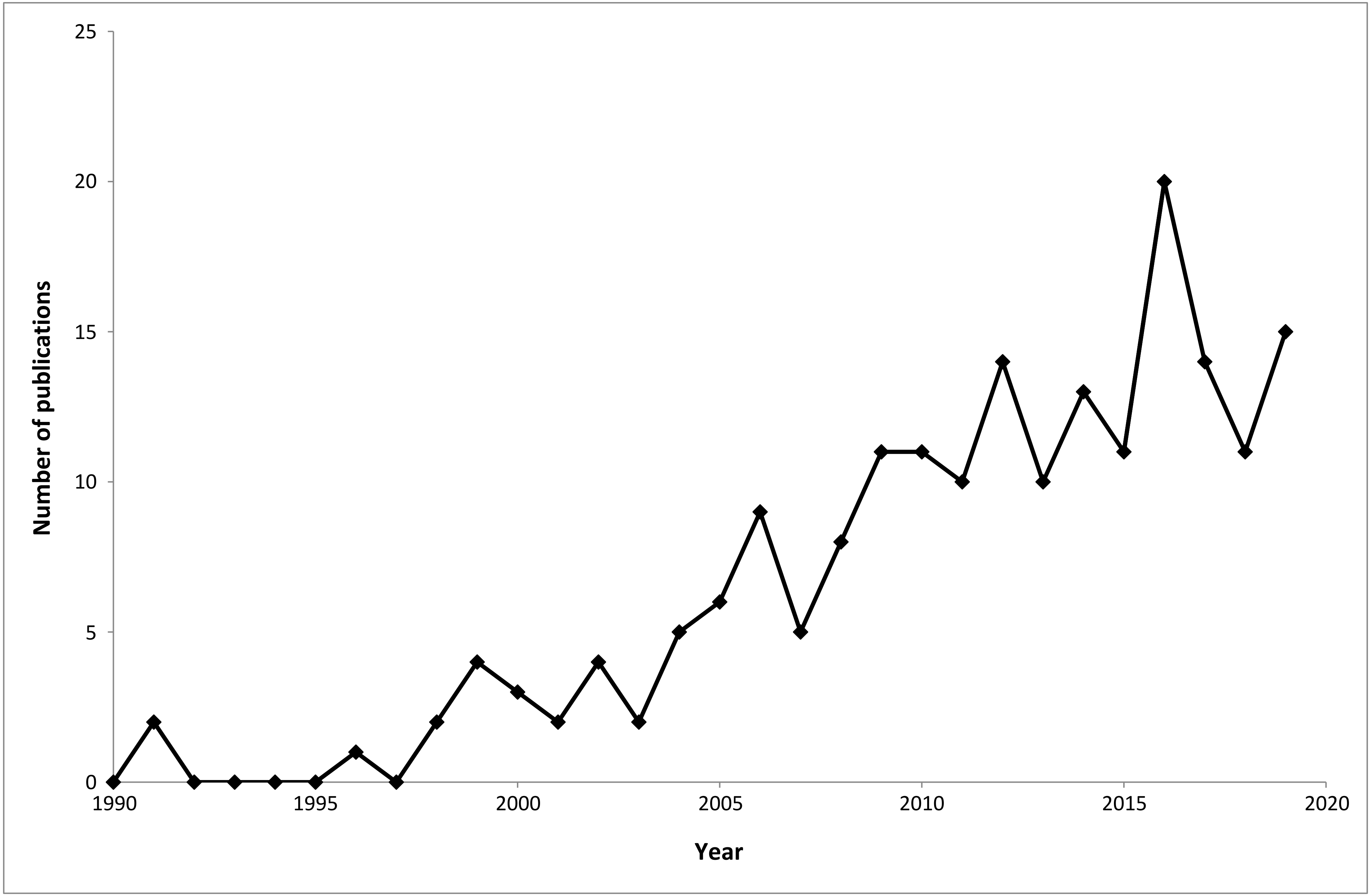
25
20
15
10
5
0
Number of publications
1990
1995
2000
2005
2010
2015
2020
Year

Year	Number of journal articles
2019	15
2018	11
2017	14
2016	20
2015	11
2014	13
2013	10
2012	14
2011	10
2010	11
2009	11
2008	8
2007	5
2006	9
2005	6
2004	5
2003	2
2002	4
2001	2
2000	3
1999	4
1998	2
1997	0
1996	1
1995	0
1994	0
1993	0
1992	0
1991	2
1990	0

Search term	**Number of publications**
Ecology	210,639
Biomechanics	193,420
Biomechanics AND (human OR sport OR animal)	153,051
Ecology AND (behavior OR behaviour)	17,763
Ecology AND physiology	12,975
Ecophysiology	5,494
"Community ecology"	4,946
"Molecular ecology"	2,209
Ecology AND biochemistry	1,895
"Chemical ecology"	1,697
Biomechanics AND plant	1,634
Biomechanics AND ecology	**294**
"Physical ecology"	12
Ecomechanics	**10**
"Mechanical ecology"	**0**