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Charles Darwin and the Importance of Biodiversity for Ecosystem Functioning

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Abstract

The link between biodiversity and ecosystem functioning is a relatively new research area motivated by forecasts of ongoing biodiversity loss. However, the intellectual link between biodiversity and ecosystem processes was first inferred by Darwin based on his «Principle of Divergence». In the notes for his «Big Species Book» Darwin explicitly states that communities composed of organisms developed under «many and widely differing forms» should have higher rates of productivity and decomposition. Darwin also cites supporting evidence in the form of the *Hortus Gramineus Woburnensis*: a grass garden at Woburn Abbey in the South of England that arguably contains the earliest known ecological experiments.

Charles Darwin und die Bedeutung der Artenvielfalt für Ökosystem-Funktionen

Die Verknüpfung zwischen Artenvielfalt und dem Funktionieren von Ökosystemen ist ein relativ neues Forschungsgebiet, welches durch den aktuellen Artenverlust und dessen Vorhersagen angetrieben wird. Die intellektuelle Verknüpfung jedoch von Biodiversität und Ökosystemprozessen wurde erstmals durch Darwin mit seinem «Divergenzprinzip» vollzogen. In den Notizen für sein «Grosses Buch über die Arten» stellt Darwin fest, dass Gemeinschaften von Organismen, die sich aus «vielfältigen und stark divergenten Formen» entwickelt haben, höhere Produktivitäts- und Abbauraten aufweisen sollten. Als wissenschaftlichen Beweis für seine Aussage nennt Darwin den *Hortus Gramineus Woburnensis:* ein Gräsergarten in der Woburn Abbey im Süden von England, welcher wohl das früheste bekannte ökologische Experiment darstellt.

Key words: **principle of divergence – ecology – ecosystem processes – George Sinclair – Hortus Gramineus Woburnensis**

Schlagwörter: **Divergenzprinzip – Ökologie – Ökosystemprozesse – George Sinclair – Hortus Gramineus Woburnensis**

1 INTRODUCTION

In the early 1980s, the disappearance of species from Earth was famously likened to the loss of rivets from an aeroplane fuselage (EHRLICH and EHRLICH, 1981). This vivid analogy played an important role in motivating ecologists to think about how changes in biodiversity affect the way that ecosystems function. Forecasts and fears of ongoing biodiversity loss (SALA et al., 2000) have sustained interest in this topic that currently goes under the heading of 'biodiversity and ecosystem functioning' (NAEEM et al., 2009). This research area properly formed in the early 1990s following a conference and the resulting edited volume (SCHULZE and MOONEY, 1993). In a chapter from this edited volume MCNAUGHTON (1993) reproduced the following quote from the Origin (DARWIN, 1859): *«It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised.»*

The quote raised several questions. First, given the early controversy over the relationship between biodiversity and ecosystem functioning (NAEEM et al., 2009) was Darwin really linking the two 150 years ago or did he mean something else? Second, because the Origin does not have a bibliography it was not clear what experimental work Darwin was referring to. In fact, the idea can be dated to the joint paper by DARWIN and WALLACE (1858) a year earlier rais-

ing the further question of whether the original idea belongs to Darwin, Wallace or both.

2 IN SEARCH OF CLUES

The first hurdle to overcome in tracking down Darwin's inspiration and source is the lack of supporting references in the Origin (DARWIN, 1859) and DARWIN and WALLACE (1858). Following Wallace's independent formulation of evolution by natural selection and their joint publication in 1858, the Origin was intended only as an abstract to a longer work. Darwin had been working on notes for his 'Big Species Book' for some time but never finished it (STAUFFER, 1959). Luckily, Darwin's incomplete notes were eventually published as Natural Selection (STAUFFER, 1975). This book is a valuable resource as it provides earlier versions for some (although not all) of the sections in the Origin complete with supporting references. The section on Darwin's Principle of Divergence in Natural Selection (corresponding to the section of chapter IV of the Origin quoted above) cites several supporting references including an article by George Sinclair (SINCLAIR, 1826) in a gardening magazine. The experiments Darwin refers to are reported as being conducted at Woburn Abbey, in South East England at the start of the nineteenth century under the supervision of George Sinclair the Duke of Bedford's head gardener. The works was originally published, in greater depth, in a book *Hortus Gramineus Woburnensis* (SINCLAIR, 1816). *Hortus Gramineus Woburnensis* was republished in several editions (including a translation into German) and in its fifth edition combined with another text by Sinclair, *The Weeds of Agriculture* (SINCLAIR, 1869).

3 THE GRASS GARDEN AT WOBURN ABBEY

The first edition of this book (SINCLAIR, 1816) describes an experimental garden designed to compare the performance of different species and various mixtures of grasses and herbs on different types of soil. A plan of the experimental garden lists the plant mixtures grown in 242 plots, each two-foot square, enclosed by boards set in cast-iron frames, with leaded tanks for aquatic species (Fig. 1). The plots were filled with selected soils or custom-made mixtures to compare the performance of the plant communities on different substrates in terms of their numbers, sizes and reproduction. These measurements of individuals and populations were accompanied by some of the earliest chemical analysis of plants and soils, guided by SIR HUMPHRY DAVY (1821).

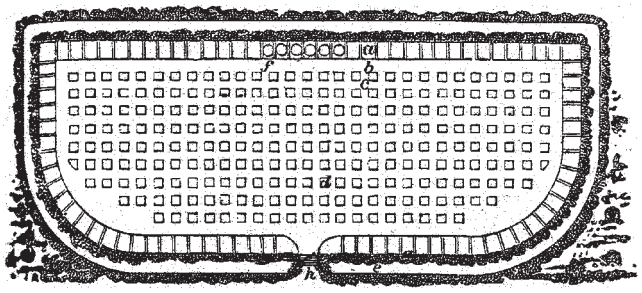

Fig. 1. A plan of the experimental plots (centre), beds (edge) and tanks (marked *f*) of the experimental grass garden taken from *Hortus Gramineus Woburnensis.*

Abb. 1. Ein Plan der Flächen (Zentrum), Beete (Rand) und Becken (markiert mit *f*) des experimentellen Gräsergartens aus dem Buch *Hortus Gramineus Woburnensis.*

The third edition of *Hortus Gramineus Woburnensis* (SINCLAIR, 1824; Fig. 2) reported that diverse transplanted turf communities were more productive than less species-rich communities established from seed (Table 1; Fig. 3), which prompted Darwin's statement that diverse differentiated communities were more productive. While the results clearly convinced Sinclair and Darwin, there are inevitably several caveats. First, the work conducted around 1820 is so early that it pre-dated the development of modern methods of experimental design and statistical analysis in the late 19th and early 20th century (STIGLER, 2003). For example, differences in diversity are confounded with differences in methodology: the communities with higher productivity and diversity are transplanted turfs while those with lower productivity and diversity were established from seed. Second, in the absence of supporting data we have to take Sinclair's assurance that, *«the weight of produce in herbage and in hay increased in proportion»* to the number of plants (SINCLAIR, 1826), although we know that the number of individuals is often uncoupled from total yield. For monocultures productivity generally increases with density only at low numbers of individuals and the plastic growth and modular nature of plants leads to a law of 'constant final yield' (KIRA et al., 1953) in which a wide range of low- and high-density mixtures reach the same end point. Nonetheless, the experiment is impressive even by today's standards. Indeed, several recent biodiversity experiments have used a similar approach.

The work also influenced the development of Darwin's 'principle of divergence', one of the building blocks for his theory of evolution by natural selection (KOHN, 1975; BROWNE, 1980). Under the principle of divergence, selection leads to new varieties arising in the same location as

they adapt to different niches. Although Darwin's main interest was on the role of natural selection in driving the evolution of differences between species, by explicitly linking diversity with productivity and decomposition Darwin (STAUFFER, 1975) also recognised the consequences of the ecological 'division of labour' (applying Adam Smith's 1776 concept in an evolutionary and ecological context) for ecosystem functioning: *«A greater absolute amount of life can be supported … when life is developed under many and widely different forms, … the fairest measure of the amount of life being probably the amount of chemical composition and decomposition within a given period.» This longer quote seems to make it clear that* Darwin clearly thought that ecological differences between species can make more diverse communities more productive.

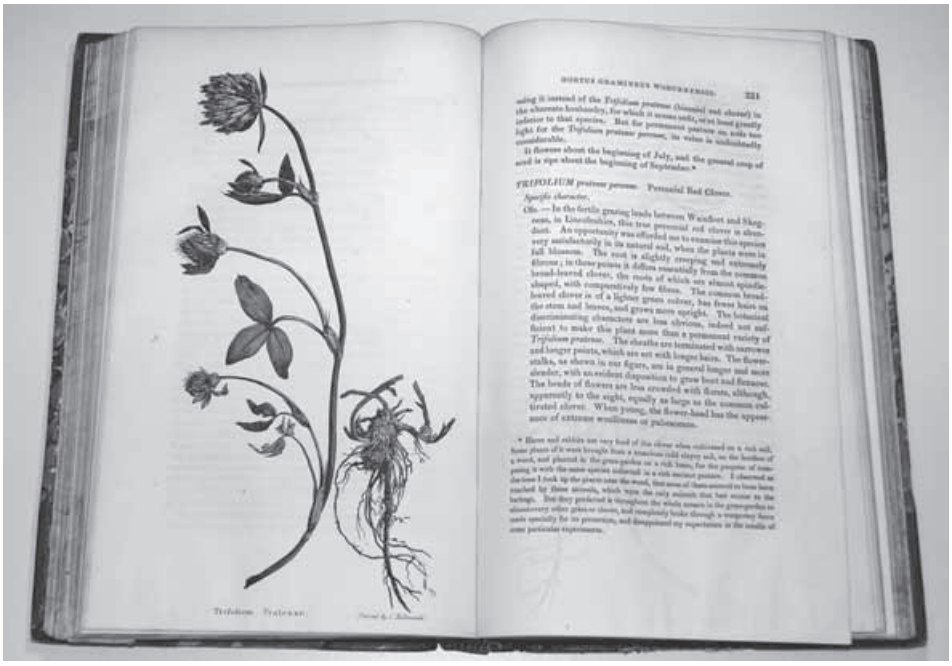

Fig. 2. A plate from the author's copy of the third edition (1824) *of Hortus Gramineus Woburnensis* showing *Trifolium pratense.*

Abb. 2. Eine Bildtafel von *Trifolium pratense* aus dem Autorenexemplar der dritten Ausgabe (von 1824) des *Hortus Gramineus Woburnensis.*

4 THE FIRST ECOLOGICAL EXPERIMENT?

In addition to its historical importance as the source of the intellectual link between biodiversity and ecosystem functioning first made by Darwin, the research from the forgotten grass garden at Woburn Abbey pre-dates all other ecological experiments that we know of. While 'ecology' was not coined until 1866 by Haeckel (ACOT, 1998) we think that the work at Woburn can be seen retrospectively as the world's first ecological experiment.

As explained above, the link between biodiversity and ecosystem functioning first attributed to Chapter IV of the Origin actually appears a year earlier in the joint publication by Darwin and Wallace in 1858. This raises the question of which author should take credit for inferring this link or whether the idea should be attributed to both authors? The clear link between diversity and functioning made by Darwin in Natural Selection (written between 1856 and 1858) suggests that, in the absence of any evidence to the contrary, the idea should be attributed to Darwin alone. I hope

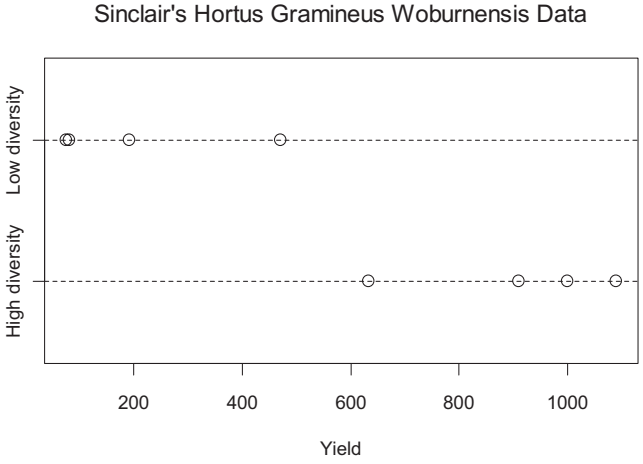

Fig. 3. Darwin's evidence: Sinclair's data from the *Hortus Gramineus Woburnensis* comparing the productivity of species rich and species poor plant communities. The number of plants per square foot serves as a surrogate for aboveground plant biomass production since «*the weight of produce in herbage and in hay increased in proportion*» (SINCLAIR, 1826, see main text).

Abb. 3. Darwins Anhaltspunkt: Die Daten von Sinclair aus dem Buch *Hortus Gramineus Woburnensis* vergleichen die Produktivität von artenarmen und artenreichen Pflanzengemeinschaften. Die Anzahl Pflanzen pro Quadratfuss (entspricht ca. 0,09 Quadratmetern) dienen dabei als Ersatz für den oberirdischen Ertrag an Pflanzenbiomasse, denn «*das Gewicht des Gras- und des Heuertrags stieg proportional an*» (SINCLAIR, 1826, siehe Haupttext).

Tab. 1. Reproduction of the table from p. 244 of the third edition of *Hortus Gramineus Woburnensis* that compares plant and species density in nine of the experimental garden plots, either transplanted natural turfs or monocultures or mixtures established from seed. Plots 1–4 appear to be natural turfs transplanted into experimental beds at Woburn, while 5–8 appear established from seed (it's unclear which applies to 9). This table is not included in the first edition, although the garden is described, and was removed from later editions to make the volume more affordable. The footnotes are our addition.

Tab. 1. Reproduktion der Tabelle auf Seite 244 der dritten Ausgabe des *Hortus Gramineus Woburnensis*, welche die Pflanzen- und die Artendichte von 9 Experimentierfeldern vergleicht. Dabei wurden entweder natürlich gewachsene Rasen umgesetzt oder Mono- sowie Mischkulturen aus Samen angesetzt. Die Felder 1–4 scheinen natürlich gewachsene Rasen zu sein, die man auf die Experimentierbeete in Woburn versetzt hat, während die Felder 5–8 angesät worden sind (es ist nicht klar, was auf Feld 9 zutrifft). Diese Tabelle erschien nicht in der ersten Ausgabe, obwohl der Garten da beschrieben wurde. Um die Ausgabe erschwinglicher zu machen, wurde die Tabelle später entfernt. Die Fussnoten wurden von uns angefügt.

	No. of distinct rooted plants or species per sq. foot			
	Total	Natural grasses	Clovers and other plants	Species
1. Richest natural pasture, grazed by 1 ox and 3 sheep per acre, from endsleigh, Devonshire.	1000	940	60	20
2. Transplanted turf of rich ancient pasture, grazed by 1 ox and 3 or 4 sheep per acre, from Croft Church, Lincolnshire.	1090	1032	58	–[*1]
3. Ancient pasture, Woburn.	910	880	30	12
4. Ancient pasture near Woburn	634	510	124	8
5. Rye grass and white clover, 3:1 mix, 2 years old, considered good of its kind.	470	452	18	2
6. Narrow-leaved meadow *grass (Poa angustifolia*), 6 years old, Woburn experimental garden.	192	192	–	1
7. Meadow foxtail (*Alopecurus pratensis*), Woburn experimental garden	80	80	–	1
8. Rye-grass (*Lolium perenne*) Woburn experimental garden	75	75	–	1
9. Water meadow, well managed, dominated by *Poa trivialis* with *Bromus arvensis*	1798	1702	96	–[*2]

[*1] presumably between 12 and 20 species
[*2] At least 3 species; *Poa*, *Bromus* and others (data point omitted from Fig. 3).

this chapter will inspire scholars of Wallace's work to investigate whether he had independently inferred the same link between biodiversity and ecosystem functioning.

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