Biodiversity Improves Life Cycle Sustainability Metrics in Algal Biofuel Production

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Supporting Information

ABSTRACT: Algal biofuel has yet to realize its potential as a commercial and sustainable bioenergy source, largely due to the challenge of maximizing and sustaining biomass production with respect to energetic and material inputs in large-scale cultivation. Experimental studies have shown that multispecies algal polycultures can be designed to enhance biomass production, stability, and nutrient recycling compared to monocultures. Yet, it remains unclear whether these impacts of biodiversity make polycultures more sustainable than monocultures. Here, we present results of a comparative life cycle assessment (LCA) for algal biorefineries to compare the sustainability metrics of monocultures and polycultures of six fresh-water algal species. Our results showed that when algae were grown in outdoor experimental ponds, certain bicultures improved the energy return on investment (EROI) and greenhouse gas emissions (GHGs) by 20% and 16%, respectively, compared to the best monoculture. Bicultures outperformed monocultures by performing multiple functions simultaneously (e.g., improved stability, nutrient efficiency, biocrude characteristics), which outweighed the higher productivity attainable by a monoculture. Our results demonstrate that algal polycultures with optimized multifunctionality lead to enhanced life cycle metrics, highlighting the significant potential of ecological engineering for enabling future environmentally sustainable algal biorefineries.

INTRODUCTION

Microalgae are promising feedstock candidates for renewable biofuel production due to their high photosynthetic efficiency, lipid content, and growth rates compared to terrestrial plants.1,2 Algae-based fuels have the potential to increase energy security, reduce fuel cycle carbon emissions, and ultimately replace petroleum-based transportation fuels. But despite decades of intensive research and development, industrial algal biofuel production has been unsuccessful.3 One major bottleneck is the difficulty in achieving the observed productivity and biomass characteristics from laboratory-scale studies in outdoor open pond raceways, which are generally deemed necessary for economic viability.4,5 In practice, production at scale has been hampered by low biomass yields, poor biomass quality, invasion by grazers, diseases, pond crashes6 and unwanted algal species,7 which are major barriers to achieving sustainability and profitability of algal biofuel production. Genetic engineering of algae and intensive management strategies such as chemical treatment with fertilizers or pesticides have shown some potential for overcoming these challenges; however, they tend to yield negative trade-offs due to either decreased algal growth or increased cost, and most have not been successfully demonstrated at scale.8–10

In terms of biofuel production, algal communities that increase overall biomass yield, as opposed to just lipid content, are ideal candidates for hydrothermal liquefaction (HTL), which converts whole algal biomass to biocrude. Ecological engineering of multispecies polycultures has been proposed as an alternative means to overcome the challenges associated with algal cultivation. On the basis of extensive research on the role of biodiversity in natural ecosystems, we know that multispecies communities of plants or microalgae can yield
more biomass, use abiotic resources more efficiently, and better resist threats such as disease, grazers, and invasive species compared to a single species. Laboratory and field studies have tested this hypothesis experimentally and found that diversity has important impacts in terms of reducing temporal variance (increased stability), nutrient use, fuel quality, and the potential to optimize multiple functions simultaneously. However, these multispecies communities rarely increase biomass yields relative to the most productive constitutive single species of the community. While these studies suggest that ecological engineering of microalgal communities is a promising strategy to improve large-scale biofuel production, it remains unclear whether these improvements make polycultures more sustainable than monocultures in terms of environmental impacts.

Here, we report results of a well-to-wheel LCA that analyzed the impact of algal biodiversity on biofuel production using both laboratory and outdoor pond cultivation data. The cohesive and comprehensive nature of the data set closes the knowledge gaps between algal cultivation, biomass conversion, and life cycle assessment, minimizing concerns of inconsistency across models and increasing industrial practicality for a more holistic algal LCA. Our results show that certain multispecies communities can outperform the best monocultures in terms of sustainability metrics under conditions that mimic real-world cultivation due to the polycultures’ superior potential for performing multiple functions well.

**MATERIALS AND METHODS**

**Algal Pond Growth.** The data used in this work stem from two published studies that have examined the role of algal biodiversity in biofuel production in both laboratory-based mesocosms and field-based open pond systems. For both of these studies, focal algal species were selected from among the high priority species determined by the U.S. Department of Energy’s Aquatic Species Program and included within the Solar Energy Research Institute’s microalgae collection. We selected six of these species: *Ankistrodesmus falcatus*, *Chlorella sorokiniana*, *Pediastrum duplex*, *Scenedesmus acuminatus*, *Scenedesmus cornis*, and *Selenastrum capricornutum*. More details on the materials and methods used in these studies can be found in the original publications.

![Figure 1. Life cycle assessment (LCA) of algal biofuel production using data from laboratory and outdoor cultivation experiments. (a) Schematic of hypothetical algal biorefinery in LCA, with flows of phosphorus, carbon, nitrogen, and water depicted as fractions of the amount leaving the first unit of Algal Pond Growth. Values shown, corresponding to line widths, represent the proportion of P, C, N, and water in the pond that flow through each step depicted in the diagram (dimensionless) and are the average fractions across all experimental conditions and culture compositions. (b) Representative microscopic images of the six microalgal species examined in this study: *Ankistrodesmus falcatus* (A), *Chlorella sorokiniana* (B), *Pediastrum duplex* (C), *Scenedesmus acuminatus* (D), *Scenedesmus cornis* (E), *Selenastrum capricornutum* (F). (c) A photo of 9.5 L laboratory mesocosms. (d) A photo of 1100 L cattle tanks simulating outdoor pond cultivation.](image-url)
falcatus (code A), Chlorella sorokiniana (B), Pediastrum duplex (C), Scenedesmus acuminatus (D), Scenedesmus ecornis (E), and Selenastrum capricornutum (F). Algal cultures were grown photoautotrophically in BOLD 3N medium sparging air without carbon dioxide supplementation. The laboratory mesocosms \( n = 180 \) were 9.5 L aquaria illuminated with fluorescent lights and diluted with 30% fresh medium every 7 days. Two distinct temperature treatments were employed to analyze the effect of temperature fluctuation on algal growth. The temperature of the tanks was either constant at 22 °C or variable between 17 and 27 °C on weekly cycles. Lab-based mesocosm experiments studied 37 combinations of algal species in two randomized blocks for each temperature treatment. Monocultures were replicated 6 times, bicultures 4 times, and four-species cultures 4 times, and the six-species polyculture was replicated 9 times for each temperature condition.17 Mesocosms were grown for 2 weeks and then measured every 7 days for a subsequent 8 weeks. The outdoor ponds experiment was performed using 80 open ponds, each 1100 L in volume and 0.5 m in depth, at the University of Michigan’s Edwin S. George Reserve, located near Pinckney Michigan.13 We used the four most productive species based on the laboratory mesocosms (A, B, D, and F) as monocultures, six two-species polycultures, and the four-

Figure 2. A Reingold-Tilford tree illustrating how information is sourced and processed within the AHM. The tree is subdivided into 41 empirical inputs (green), 19 process specifications (blue), and 28 assumptions (beige). Internal calculations (red) combine the values from the other categories to derive LCA metrics. Inputs marked with a (*) were used in multiple calculations. Plot developed using Data-Driven-Documents.24
Hydrothermal Liquefaction. Many strategies have been developed to produce usable fuel from algae, ranging from transesterification of fatty acid methyl esters, liquid—liquid extraction, and hydrothermal liquefaction (HTL). More recently, focus has shifted toward HTL of algal biomass, a strategy that employs high temperature (200–400 °C) and pressure (2–20 MPa) to convert whole algal biomass into biocrude rather than only lipids into biodiesel.19 The coproducts of HTL include solid biochar, nutrient-rich aqueous phase, and gases. Laboratory HTL experiments were conducted using harvested biomass at 5% dry mass loading at 350 °C for 20 min.16 The 5% mass loading was scaled to the 15% from algal dewatering for more energetically favorable biomass conversion. Slurries above 15% demonstrate non-Newtonian behavior at operating temperatures and were not considered.20 Heating values of biocrude samples were calculated from elemental composition using the Channiwalla formula.21 Upgrading methodology then followed Frank et al. (2013) for carbon mass balance efficiency during deoxygenation and denitrogenation, which differ between cultures due to variable biocrude oxygen and nitrogen content.22 Upgraded biocrude is assumed suitable as a diesel fuel. Recycling, dewatering, and infrastructure are described in more detail in SI 1.

Life Cycle Assessment Overview. A computational module of algal cultivation and life cycle inventory was established based on our empirical data, which we called the algal hydrothermal liquefaction module (AHM). The AHM is broken down into six stages: algal pond growth, first dewatering, remaining dewatering, biomass conversion, upgrading, and infrastructure. The biomass conversion phase is divided into hydrothermal liquefaction (HTL) and catalytic hydrothermal gasification (CHG). To compare algal polycultures and monocultures, we employed the AHM to simulated a hypothetical biorefinery system (Figure 1a), using a large experimental data set generated previously through multidisciplinary work involving six algal species (Figure 1b) that were grown alone or in mixed species consortia in replicated laboratory mesocosms (Figure 1c) and open outdoor ponds (Figure 1d).15–17,23

The AHM calculations use a functional unit of 1 g of ash free dry weight (afdw) algae and, where necessary, employ realistic and documented assumptions to scale experimental data to an industrial-sized facility. The AHM quantifies properties and functions of the algal biorefinery system, including biomass concentration, productivity, crop stability over time, biocrude and biomass elemental composition, efficiency of abiotic nutrient use, and biocrude yield. Figure 2 illustrates the various assumed, specified, and empirical inputs as well as their incorporation in the multilayered calculations within AHM (see Table S1 for details).

Values from the AHM were then utilized as inputs to the Greenhouse gases, Regulated Emissions, and Energy in Transportation (GREET) impact assessment model developed by the Argonne National Laboratory25 using a functional unit of 1 MBTU (10^6 BTU) transportation energy in compression ignited direct injection diesel vehicles.26 The GREET utility is a versatile tool updated biannually that computes greenhouse gas emissions (CO₂, CH₄, N₂O), nonrenewable energy usage, as well as six standard pollutants: carbon monoxide, mononitrogen oxides, sulfur oxides, volatile organic compounds, and particulate matter (PM₁₀ and PM₂.₅) for many fuel/vehicle systems.25 GHGs are normalized to CO₂ eq using global warming potentials established by the Intergovernmental Panel on Climate Change ARS.27
as percentages relative to compression ignited direct injection diesel vehicles fueled with conventional diesel. To be considered a sustainable fuel, a biofuel must have an EROI higher than 1.0 and GHGs must be lower than conventional diesel, estimated at 99.5 kg CO₂ eq per MBTU on a well-to-wheel basis. In most cases, there is a negative correlation between GHG and EROI: increasing productivity increases the footprint by decreasing nonrenewable energy consumption. Rather than using arbitrary values to conduct a sensitivity analysis of parameters, as is commonplace among LCAs, we examined empirical variation in Monte Carlo simulations using a truncated standard distribution. Using this method, values of inventory inputs are varied simultaneously for an accurate representation of the data set. Regression coefficients were generated by using 5000 Monte Carlo simulations with the highest EROI to quantify the influence of variation in inventory inputs on impact assessment outputs. We used this approach because life cycle metrics are inherently nonlinear at low values of inputs like productivity and biomass concentration, which reduces fit dramatically.

## RESULTS AND DISCUSSION

### Single Highly Productive Monoculture Was the Top Performer in Maximizing EROI and Minimizing GHGs (on the Basis of Lab Data).

We first applied the LCA framework described above to data collected from a set of experiments where a total of 37 algal cultures, including 6 monocultures and 31 select polycultures, were grown in the laboratory at a constant temperature of 22 °C and then converted to biocrude oil through HTL. Figure 3 summarizes results for two LCA metrics, EROI and GHGs.

In this assessment, a monoculture, *S. capricornutum* (F), and this species in bicultures with *A. falcatus* (AF) or *P. duplex* (CF) were the best performers, generating EROIs of 0.99, 0.72, and 0.64 as well as GHGs of 122, 120, and 135 kg CO₂ eq per MBTU, respectively. Water intensity, which represents the net water usage per MBTU fuel produced, was determined to be 172, 165, and 150 L/MBTU, respectively (Figure S1). Water intensity, which represents the net water usage per MBTU fuel produced, was determined to be 172, 165, and 150 L/MBTU, respectively (Figure S1). Water intensity, which represents the net water usage per MBTU fuel produced, was determined to be 172, 165, and 150 L/MBTU, respectively (Figure S1).

Closer examination of the results revealed that *S. capricornutum* (F) cultivation yielded the best sustainability metrics due to its ability to achieve a high biomass concentration of 0.37 g/L, which was nearly three times higher than the average of all cultures under these experimental conditions (0.13 ± 0.08 g/L) and substantially better than the second-best culture AF (0.30 g/L). In another set of laboratory experiments, the same algal cultures were grown under variable temperature conditions, where the temperature cycled between 17 and 27 °C on a weekly basis. We also performed an LCA based on data collected from these experiments (Figures S1, S2), and our results followed the same general pattern obtained using constant temperature data, with the best performers in EROI again being *S. capricornutum* and its bicultures. It was noted that the variable temperature condition had no significant impact on biomass concentration, biocrude yield, or stability.

Nonrenewable energy usage was partitioned by stage of production to identify areas for optimization as illustrated in Figure 4.

Algal growth and first dewatering dominated process energetics with a minimum fraction of approximately 60% of the total energy for *S. capricornutum*. The subsequent factors were infrastructure (14.3%), transportation and distribution (11.3%), and biocrude conversion (4.1%). These results confirm that even for the best performing algal species, the greatest gains to advancing biofuel sustainability could be made by optimizing cultivation conditions and minimizing upstream energy inputs.

### Select Bicultures Outperformed the Top Monoculture in Outdoor Ponds.

We next used data collected from an outdoor cultivation experiment, where a total of 11 promising algal cultures, including 4 monocultures, 6 bicultures, and 1 four-species culture, were grown in 1100 L open ponds (6–8 replicates). It should be pointed out that scaling of experimental data to large-scale cultivation introduces uncertainties, particularly related to how parameters like productivity and biomass accumulation change in actual raceway pond cultivation compared to experiments. Here, we have made an effort to minimize these uncertainties by incorporating empirical data from experiments performed under conditions that mimic real-world conditions. Specifically, the outdoor pond cultures were subject to environmental realities including fluctuations of photosynthetically active radiation (PAR), invaders, temperature change, evaporation, etc. These data on biomass cultivation were supplemented with elemental data and biocrude yields from variable temperature mesocosm experiments to capture characteristics of outdoor pond cultivation, encompassing physiological changes in elemental composition due to varying temperature as well as...
mitigated growth due to exposure to naturally occurring invaders, variable sunlight, and other environmental factors. Figure 5 shows LCA results on two metrics based on outdoor condition. Intriguingly, in this analysis, bicultures BF and AF outperformed *S. capricornutum* (F) in terms of EROI, GHGs, and WI (*p* < 0.05). EROI for cultures BF, AF, and F were 0.60, 0.54, and 0.51, respectively, representing a significant 20% improvement by the best biculture BF over the best monoculture F. For GHGs, cultures BF, AF, and F led to values of 137, 154, and 163 kg CO₂ eq/MBTU, respectively, marking a 16% improvement by biculture BF in comparison to monoculture F. Water intensity (WI) results followed those of GHGs with values of 268, 364, and 444 L/MBTU (Figure S4).

The apparent success of bicultures BF and AF is contrary to what was observed in the laboratory experiments in which *S. capricornutum* outperformed the next best culture in EROI by a 27% margin. The average biculture also outperformed the average monoculture and the four-species culture in each life cycle metric (*p* < 0.05). We noted that despite lower performances in EROI, GHGs, and WI compared to those in two bicultures BF and AF, *S. capricornutum* maintained the highest biomass concentration and productivity of all cultures with 0.200 g/L and 9.24 g/m²/day, far greater than BF and AF at 0.143 g/L and 6.45 g/m²/day and 0.16 g/L and 7.54 g/m²/day, respectively. However, the extent of these advantages of *S. capricornutum* under outdoor conditions were considerably smaller than those under laboratory conditions. In terms of biomass productivity, *S. capricornutum*’s advantage over the bicultures AF and BF decreased from 48% (laboratory) to 19% (outdoor) and from 137% to 59%, respectively. With regard to biomass concentration at harvest, *S. capricornutum*’s advantage over the bicultures AF and BF decreased from 45% (laboratory) to 21% (outdoor) and from 126% to 48%, respectively.

The disparity between *S. capricornutum*’s superiority in biomass concentration/productivity and its inferiority in LCA metrics, compared to those in bicultures BF and AF, indicated that the positive impact of biomass production was outweighed by other aspects of *S. capricornutum* that negatively impacted LCA metrics. For instance, we noted that *S. capricornutum*...
demanded significantly higher phosphorus inputs at 2.93 mM P/g afdw algae, compared to 1.7 mM P/g afdw for BF and 2.1 mM P/g afdw for AF. Higher P requirements adversely affected overall life cycle metrics. Intriguingly, this high demand for phosphorus was not apparent under the constant temperature mesocosm condition in the laboratory, suggesting physiological differences between algal growth under the constant temperature condition and the outdoor pond condition. We further hypothesized that select polycultures outperformed the best monoculture by maintaining multiple functions in a more balanced manner, an effect of biodiversity referred to as multifunctionality. In particular, the two most productive species C. sorokiniana and S. capricornutum, have disparate N and P nutrient use efficiencies. When grown together, these species simultaneously optimize N-efficiency, P-efficiency, and biomass production better than either species can as a monoculture. Thus, while S. capricornutum dominated in terms of stability, productivity, and biomass concentration across all experimental conditions, these factors were outweighed by nutrient use efficiency under outdoor pond conditions, compared to those in bicultures AF and BF.

Superior Multifunctionality of Polycultures Leads to More Favorable Life Cycle Metrics. To systematically dissect how multifunctionality benefited bicultures BF and AF, compared to the best monoculture F, we conducted a multilinear regression analysis to quantify how different aspects of performance impact LCA metrics. Independent input variables included nutrient recycling, elemental composition, biocrude yields, biomass concentration, and frequency of crashes from outdoor pond experiments. Dependent inputs such as productivity and H/C ratios were excluded as, for example, biomass concentration is strongly correlated with calculated productivity (SI 1) ($R^2 = 0.99$). Each input was normalized using Z-scores such that regression coefficients provide relative weights for individual inputs with respect to EROI ($\sigma_{\text{EROI}}/\sigma_{\text{input}}$)

$$
\left( \frac{Y_i - \bar{Y}_i}{\sigma_i} \right) = \beta_0 + \sum_{j \neq i} \beta_i \times \left( \frac{X_j - \bar{X}_j}{\sigma_j} \right) + \epsilon
$$

The multilinear regression yielded a good fit to the data ($R^2_{\text{EROI}} = 0.78$) using the workflow depicted in Table 1. The product of an input regression coefficient and its Z-score yielded its contribution to the EROI. The aggregation of these contributions then yielded the overall sustainability impact. Predicted EROI values corroborated actual EROI from GREET within reasonable deviations. GHGs ($R^2_{\text{GHG}} = 0.75$) and WI ($R^2_{\text{WI}} = 0.92$) regressions were also conducted and were inversely correlated to EROI (Table S3, S4).

Results from the regression analysis showed that biomass concentration, “Biomass Density” in Table 1, is the single most important aspect of performance; however, biocrude yield, biocrude and algal elemental compositions, and nutrient use efficiencies also have significant effects on sustainability metrics. Changes in dry algal biomass P ($\beta = 0.05$) and N ($\beta = 0.01$) have minimal effects on EROI whereas changes in biomass concentration ($\beta = 1.15$) and recovered phosphorus ($\beta = 0.65$) have large effects (Table S2). Despite the importance of individual aspects of performance such as biomass concentration, the net impact of different algal culture compositions depends upon the balance of positive impacts from above-average functions/trait and negative impacts from below-average functions/trait. As a result, culture compositions that have high Z-scores for multiple functions can outperform compositions that perform only one or two functions well but perform other functions poorly. In our system, the best single species (S. capricornutum) had a strong positive impact on LCA metrics based on its ability to achieve high biomass concentration ($+1.88 \sigma_{\text{EROI}}$), but this advantage was largely negated by poor phosphorus nutrient use efficiency, which decreased EROI by $-1.25 \sigma_{\text{EROI}}$. Conversely, two bicultures that had lower biomass production (BF and AF) exhibited high efficiency of nutrient recycling from the exhausted medium and aqueous coproduct (ACP) from hydrothermal liquefaction, accounting for 0.63 and 0.21 $\sigma_{\text{EROI}}$ respectively, (compared to $-1.11 \sigma_{\text{EROI}}$ for species F). The result of these impacts is that the best single species, F, has an EROI of 0.51 whereas the best polyculture, BF, has an EROI of 0.60 (an increase of 18%). ![](https://example.com/image.png) Among these inputs, S. capricornutum and many monocultures alike tend to have imbalanced impact contributions such that, in this case,
adept biomass accumulation but poor phosphorus nutrient use efficiency ultimately yield worse sustainability metrics.

Figure 6 illustrates how this effect of multifunctionality led to the superior performance of bicultures BF and AF, over the best monoculture F. Thus, using data collected under realistic outdoor open pond conditions, our results highlight how biodiversity improved life cycle sustainability metrics in algal biofuel production. Our study shows that biodiversity can improve sustainability of algal biofuel due to the ability of polycultures to optimize multiple functions simultaneously that influence LCA metrics. This is a key finding for the development of sustainable biofuel systems as it shows that polycultures can help overcome the intense trade-offs that are characteristic of single-species cultivation.

While some previous LCAs have indicated that algal biofuels could attain EROI > 3.0, our assessment indicated that algal biocrude production, at its current R&D stage, would not be energetically favorable. Numerous input and design factors are known to impact the outcome of LCAs, but we believe that the comparatively lower EROI from our LCA is due to the fact that we parametrized biomass and productivity data from outdoor experiments, whereas many other assessments have assumed rates of productivity and biomass concentrations that are higher than what is typically measured in such experiments. In fact, other assessments that were based on experiments under more realistic conditions have also produced more modest estimates of life cycle metrics. Another important distinction is that our LCA acknowledges that biomass concentration and areal productivity are not independent variables (SI 1 Materials and Methods). To demonstrate the combined impact of biomass concentration and areal productivity on EROI, we conducted a simple calculation comparing the performance of *S. capricornutum* using our own empirical values (mean of 6.25 g/m²/day and 0.37 g/L) versus the performance with assumptions commonly ranging estimates of algal life cycle metrics.38 Recent meta-analyses and harmonization reports have suggested standardized input values, but whether those standardized assumptions match typical outdoor cultivation data remains unanswered.3,39–41 Validation of assumptions and determination of life cycle metrics will require multidisciplinary research and development that closes the knowledge and expertise gaps between algal cultivation, biomass conversion, and life cycle assessment.

The development of renewable fuels from algae also faces the challenge of scaling from small experiments to large commercial cultivation systems. Our assessment indicates that biodiversity can improve sustainability metrics based on data from 1100 L scale outdoor cultivation experiments, but further study using large-scale cultivation (e.g., commercial raceway ponds) is required to know whether those benefits outweigh potentially lower productivity of polycultures. The problem of scalability is not unique to our study but is a pervasive issue for all algal biofuel work and will require more rapid transition from small-scale experiments to large outdoor raceways or photobioreactors that mimic mature biorefineries. The superior potential for multifunctionality of certain polycultures compared to the best monoculture as demonstrated in this assessment suggests that the widely employed strategy of selecting strains based on potential productivity or lipid content is inadequate for determining the sustainability or suitability of an algal feedstock. Specifically, choosing a species based on its productivity may maximize the rate of biofuel production, but that single measure of performance often comes at the expense of other important aspects of performance (e.g., nutrient use efficiency, biomass composition). Notwithstanding engineering improvements to cultivation systems and downstream technologies, our assessment shows how ecological engineering of algal communities can optimize multiple functions simultaneously, which is critical for the production of algal biofuels as a sustainable and competitive alternative to petroleum-based fuels.

### ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge on the ACS Publications website at DOI: 10.1021/acs.est.9b00909.

Elaborated description of methods and materials for each stage of the LCA including a more detailed description of pond crash calculations (PDF)

AHM framework and Monte Carlo results for each algal culture and condition (XLSX)

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**Notes**

The authors declare no competing financial interest.

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