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MICROALGAL BIOFUEL PRODUCTION SYSTEMS: ENVIRONMENTAL ASPECTS AND IMPACTS ON BIODIVERSITY

Diego Felipe Correa Gómez

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PRELIMINARY PAGES

ABSTRACT

If humanity aims to avoid further biodiversity losses and environmental degradation, future energy demands must be met through the use of more sustainable energy production systems. Biofuels have been proposed as a more sustainable alternative for energy production as, under several cultivation conditions, they reduce greenhouse gas emissions and facilitate carbon recycling over much shorter time frames than fossil fuels. However, several environmental impacts have been linked to biofuel production, particularly when their cultivation competes with food production and biodiverse lands.

Microalgal production systems may become a more sustainable option for the production of biofuels, as a result of their high yields per unit area, their potential to use different types of water (freshwater, brackish water, and seawater), their non-dependence on arable lands, and their potential to use wastewater and CO_2 from industries. This project evaluates the several potential environmental impacts of microalgal liquid biofuel production systems compared to first generation biofuels (i.e., food crops such as maize, sugarcane, soybeans, and oil palm), with a focus on vertebrate biodiversity. Additionally, it identifies cost-effective areas for siting microalgal production farms globally, in which profitability is maximized and direct competition with food production and biodiverse areas is minimized. Finally, it evaluates how novel and more sustainable biofuel production systems can be implemented in order to gradually replace less sustainable biofuel production systems, which include those based on food crops.

This work improves the understanding of the potential synergies and trade-offs between microalgal biofuel production, agricultural production, and biodiversity conservation at global and regional scales. Furthermore, it provides a framework for identifying best areas for siting microalgal biofuel production farms globally based on targets in energy demands. Microalgal biofuel production systems can help humankind achieve ambitious targets in energy production with lower environmental impacts than first generation biofuels, mainly in terms of reduced land-use changes within high-value agricultural areas and biodiverse lands.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, financial support and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my higher degree by research candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications included in this thesis

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Contributions by others to the thesis

Profs. P.M. Schenk and H.P. Possingham contributed to the conception, design, and critical revision of chapters. Dr. H.L. Beyer contributed to the conception, design and critical revision of each chapter, and in guiding the analyses and interpretation of research data. Dr. S.R. Thomas-Hall provided technical advice. Dr. J.E. Fargione and Prof. J.D. Hill contributed to the design and critical revision of Chapter 3 and 5, and in guiding the analyses and interpretation of research data in these chapters. Dr. J. García-Ulloa contributed in guiding the analyses and interpretation of research data in Chapter 4.

Statement of parts of the thesis submitted to qualify for the award of another degree

No works submitted towards another degree have been included in this thesis.

Research involving human or animal subjects

No animal or human subjects were involved in this research.

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How plain would life become without mystery, discovery, and change. I want to quote Carl Sagan from one of his several books, The Demon-Haunted World: “It is far better to grasp the Universe as it really is than to persist in delusion, however satisfying and reassuring”. I could not agree more with this idea.

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Biofuel, bioenergy, microalgae, environmental impacts, biodiversity, agriculture, sustainability, biodiesel, carbon, climate change.

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In memory of Virginia Trujillo and León David Arias

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List of Abbreviations used in the thesis

EU: European Union
GIS: Geographic Information Systems
GJ: Gigajoules
GNI: Gross National Income
Gt: Gigatonnes
ha: Hectares
L: Liters
kg: Kilograms
kL: Kiloliters
km: Kilometers
m: Meters
mboe: million barrels of oil equivalent
MCDA: Multiple-Criteria Decision Analysis
Mg: Megagrams
MODIS: Moderate Resolution Imaging Spectroradiometer
MTOE: Million Tonnes of Oil Equivalent
OECD: Organization for Economic Co-operation and Development
USA: United States of America
USD: United States Dollar

INTRODUCTION

In 2040 energy demands could increase by 28% compared to 2016, even under the implementation of policies for the increased use of renewable energy sources (IEA 2017). This could further increase environmental degradation, by impacting essential global systems such as climate, food production, and biodiversity (Rockström et al. 2009), and by impacting the provision of multiple ecosystem services (Balvanera et al. 2001, MEA 2005). How humanity will reach its future energy demands while halting environmental degradation remains as a major current challenge.

The replacement of fossil fuels by renewable energy systems has been outlined as the main way to meet growing global energy targets while preventing further environmental degradation through the reduction of greenhouse gas emissions (Goldemberg 2006, Panwar et al. 2011, IPCC 2015). Biofuels, which derive from biomass transformation, have been proposed as a more sustainable alternative for energy production compared to fossil fuels—particularly for replacing liquid fuels in the transport sector (Fulton et al. 2015)—as in theory, their production and use should not increase the net atmospheric CO_2 contents (McKendry 2002, Naik et al. 2010). However, several environmental impacts of biofuel production systems have been widely debated (Fargione et al. 2010, Fletcher et al. 2011, Castanheira et al. 2014, Immerzeel et al. 2014). In particular, the conversion of native ecosystems into biofuel crops result in the local extinction of species, negatively impacting biodiversity (Koh 2007, Duke et al. 2013, Pedroli et al. 2013, Mukherjee and Sovacool 2014), and in the emissions of vast amount of greenhouse gasses (Fargione et al. 2008, Searchinger 2010). This can occur when biofuels derive from food crops (i.e., from first generation biofuels), which need fertile soils and thus compete with agricultural lands and biodiverse areas (Fargione et al. 2010, Immerzeel et al. 2014, Correa et al. 2017).

Currently, most liquid biofuels are produced in the forms of ethanol and biodiesel, with around 87.2 billion liters of ethanol and 26.3 billion liters of biodiesel produced in 2013 (REN21 2016). The USA and Brazil lead in ethanol production, mainly from maize and sugarcane, respectively; while the EU-27 leads in biodiesel production, based on a wide arrange of oilseeds (e.g., soybeans, rapeseed, and oil palm) (RFA 2014, REN21 2016). This production overlaps with areas of high agricultural and ecological importance (e.g., the temperate grasslands in North America, the Cerrado savannas in Brazil, and the tropical rainforests in Southeast Asia), competing with food production and biodiversity conservation (Fargione et al. 2009, Morefield et al. 2016, WWF 2016). With an expected increase of between 6% and 16% in total transport energy demands supplied by biofuels by 2040 (IEA 2017), the implementation of more sustainable biofuel production alternatives should be considered.

Several solutions have been proposed to reduce the environmental impacts exerted by biofuel production systems. These include the adoption of systems that can be produced in non-arable lands, which would avoid conflicts with food production and biodiverse areas (Tilman et al. 2009). The use of third generation biofuels, which derive from microalgae, has been considered as a promising sustainable alternative compared to food crops. Microalgal production systems do not depend on arable lands, they offer higher yields per unit of area, different species and strains can be selected to grow in different types of water (freshwater, brackish water, or seawater), and they have the ability to recycle nutrients found in wastewater systems and to absorb CO_2 emissions from industries and other polluting sources (Chisti 2007, Schenk et al. 2008, Wang et al. 2008, Brennan and Owende 2010, Mata et al. 2010, Christenson and Sims 2011, Pittman et al. 2011).

However, it is not well understood how microalgal biofuel production systems may impact food systems and biodiversity in comparison to first generation biofuels. Furthermore, little is known about the optimal siting of microalgal production farms that maximize their profitability but also minimize their direct competition with high-value agricultural lands and biodiverse areas.

This project aims to assess the potential impacts of microalgal liquid biofuel production systems on food production and biodiversity compared to first generation biofuels and with focus on vertebrate species. Analyses are based on open raceway ponds, which are currently considered the most cost-effective technology for microalgal cultivation (Schenk et al. 2008, Slade and Bauen 2013). In particular, this project aims to assess the direct and indirect impacts of biofuel production on biodiversity, comparing first generation biofuels with microalgal production systems within tropical and subtropical regions of the world and focusing on vertebrates (Chapter 1). Additionally, it aims to provide insights into best geographical locations for the potential deployment of microalgal production farms where profitability is maximized and direct competition with agricultural systems and biodiversity are minimized, considering targets in global (Chapter 2) and national energy demands (Chapters 3 and 4). A particular emphasis has been placed on tropical and subtropical regions of the world, which not only hold most of global biodiversity (Valencia et al. 1994, Dirzo and Raven 2003, Kier et al. 2005), but also offer a great potential for future agricultural and biofuel expansion and intensification (Laurance et al. 2014). Finally, it aims to provide considerations for identifying and implementing more sustainable biofuel production alternatives (Chapter 5).

Following the introduction and general context section—which include the rationale and aims of the thesis, as well as background information—the dissertation is structured into five chapters (Fig. 1). The aims of each of the six chapters are as follows:

- Assess the direct and indirect impacts of biofuel production on biodiversity, comparing first generation biofuels with microalgal production systems in tropical and subtropical regions of the world and focusing on vertebrates.

- Determine which are the most suitable areas in the world for microalgal cultivation, while maximizing profitability and minimizing direct competition with food production and biodiversity and considering global energy targets.

- Determine in which countries microalgal biofuel production could be scaled up for fulfilling current and future domestic transport energy demands without significantly impacting agricultural and natural systems.

- Assess the potential conflicts among microalgal cultivation, food production, biodiversity conservation, and carbon storage for fulfilling future domestic targets in transport energy demands within four Neotropical countries (Panama, Colombia, Ecuador, and Venezuela) when compared to oil palm and sugarcane production.

- Propose how microalgal biofuel production systems and other novel and sustainable biofuel production alternatives could be identified and implemented.

The first chapter synthesizes current research on the environmental impacts of first generation biofuels, and provides insights on the potential impacts of microalgal biofuel production on biodiversity. It also compares the amount of land that would be needed to satisfy each country's gasoline and distillate fuel oil demands by using microalgae or the best bioethanol and biodiesel crop per country, offering a direct comparison on their relative ecological footprint in terms of cultivation land.

The second chapter explores locations globally where microalgal biofuel production systems could be scaled up without directly competing with areas of high agricultural and biodiversity value. It also explores potential trade-offs between microalgal cultivation, food production, and biodiversity conservation based on targets on energy demands.

The third chapter explores best locations for microalgal biofuel production at national scales, considering current and future national targets in domestic biofuel production. It offers insights on countries where microalgal biofuel production can be scaled up without directly competing with areas of high agricultural and biodiversity value.

The fourth chapter compares best areas for reaching future domestic targets in energy production in Colombia, Ecuador, Panama, and Venezuela, based on microalgal, oil palm, and sugarcane cultivation. It provides insights on potential future conflicts among biofuel cultivation, food production, biodiversity, and carbon storage within these four Neotropical countries, where agricultural expansion threatens areas of global ecological importance.

The fifth chapter provides information on how more sustainable biofuel production systems, including microalgae, can be identified and implemented. Additionally, a set of strategies for decreasing the economic barriers that prevent the implementation of more sustainable biofuel production systems is provided.

The final section synthesizes the results and caveats found throughout this thesis and offers guidance on future work in the fields of biofuel production systems and their sustainability.

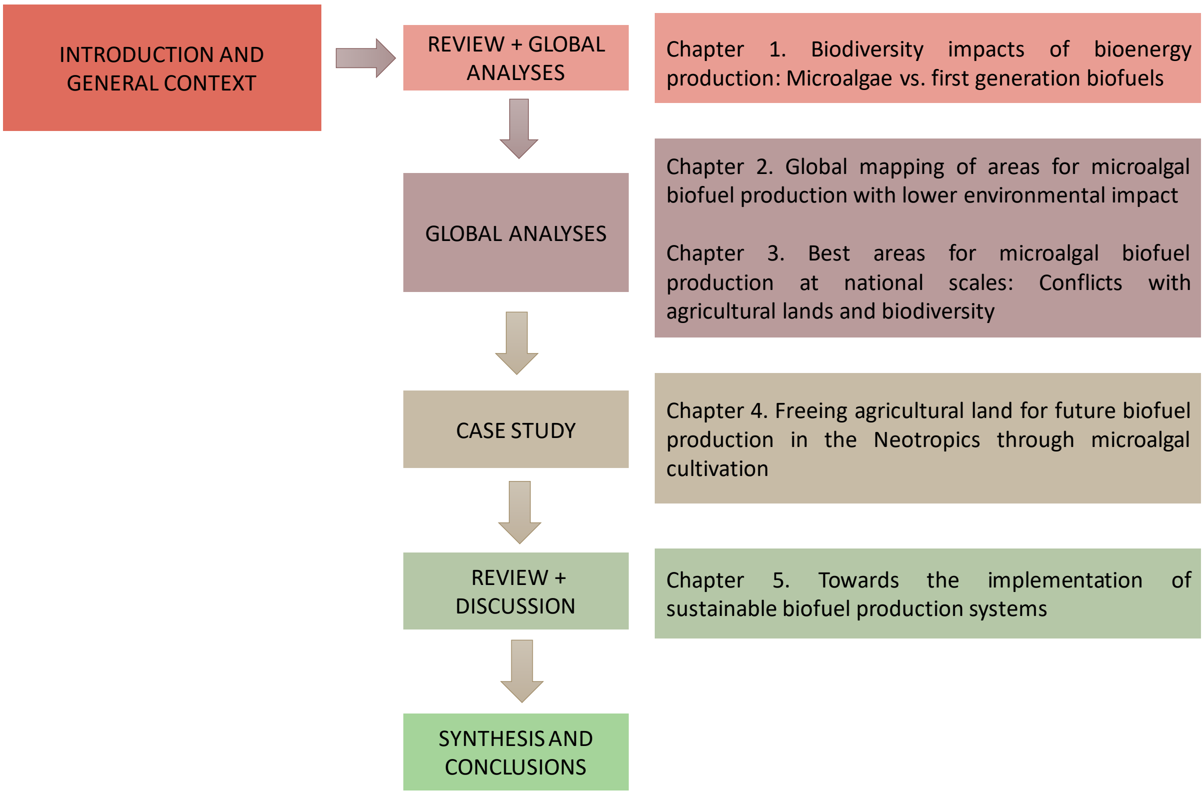

Figure 1. Structure and chapters of the thesis.

GENERAL CONTEXT

1. Current and future energy demands

In 2016 around 13,760 Million Tonnes of Oil Equivalent (MTOE) were consumed around the world (IEA 2017), mainly derived from fossil fuel sources (i.e., 81 %), followed by renewable sources and nuclear energy (i.e., 14% and 5%, respectively) (IEA 2017). With around 30% of total final energy consumption, and 55% of total oil consumption—in the forms of gasoline and diesel for road transport, kerosene for aviation, and heavy fuel oil for navigation—the transport sector was a main greenhouse gas emitter (i.e., nearly 23% of total CO_2 emissions in 2016 among production sectors) (IEA 2017), driving global warming and environmental degradation (Rockström et al. 2009).

Global energy demands are expected to increase as a result of the ongoing global population and economic growth, especially in developing economies. Under a central scenario of economic and population growth, global energy demands are expected to increase by 28% between 2016 and 2040, reaching to 17,584 MTOE, mainly driven by Asian, African, Middle Eastern, and Latin American countries. This central scenario considers policies and measures that have been adopted and proposed until mid-2017, and thus, includes the proposed support for renewable energies, increased energy efficiency, and alternative fuels. Under a scenario for reduced climate change (i.e., Sustainable Development Scenario, equivalent to the former 450 Scenario), in which global warming is limited to below 2°C compared to pre-industrial levels, total energy demands are expected to increase by only 2% from 2016 to 2040. However, under this scenario, biofuel consumption would be highest, with an estimated increase from 1.7 mboe day^{-1} in 2016 to 8.1 mboe day^{-1} by 2040 (i.e., from 3% to 16% of total transport energy consumption between 2016 and 2040) (IEA 2017).

2. Current and future food demands

Future food demands are expected to increase, driven by population growth, increased GDP, and change in food habits (e.g., increasing meat consumption in developing countries). At a population projection of around 9 billion people by 2050, it is expected that food production should increase by

60%. This increase in food production is expected to occur not only as a result of improved yields (Long et al. 2015) but also through agricultural intensification and expansion of agricultural lands around the world (Alexandratos and Bruinsma 2012).

According to the Global Agro-Ecological Zones model (FAO 2018), there are 7.2 billion hectares that can be suitable for food production. Of these lands, only around 1.6 billion are currently used for crop production and an additional 75 million hectares are used for agriculture in lands classified as unsuitable but using irrigation. After excluding forests, protected areas, other land-uses (e.g., urban areas), and areas with low suitability for agricultural production, around 1.4 billion hectares remain for further agriculture expansion. Within these areas, agriculture is expected to expand by around 70 million hectares by 2050, especially in developing countries in tropical areas (Alexandratos and Bruinsma 2012, Laurance et al. 2014), which harbor most of global biodiversity (Pimm and Raven 2000, Dirzo and Raven 2003).

3. Conservation of biodiversity and environmental degradation

Biodiversity—a fundamental component of ecological systems—is currently under threat, mainly driven by the anthropogenic habitat destruction (Pimm and Raven 2000, Lawler et al. 2006, Rockström et al. 2009), but also affected by climate change, habitat pollution, and occurrence of invasive species (MEA 2005). Biodiversity losses diminish the capacity of ecosystems to withstand environmental pressures and disturbances (Tilman et al. 2006, Oliver et al. 2015), leading to the alteration in the provision of multiple ecosystem services in which humans rely (Costanza et al. 1997, MEA 2005). For instance, biodiversity losses can diminish freshwater provision, decrease soil fertility, decrease the provision of species that could be used for treating illnesses, and alter patterns in the transmission of diseases (MEA 2005, Foley et al. 2007).

Average extinction rates during the past 100 years are considered to be at least 100 times greater compared to fossil records (Ceballos et al. 2015). In fact, according to the IUCN red list around 26% of mammals, 13% of birds and 41% of amphibians are under any threat category (IUCN 2016). Additionally, 9 of the 14 world biomes have been transformed into croplands in around 20% to 50% of their original extent; being tropical dry forests, temperate grasslands, temperate broadleaf forests, and Mediterranean forests, the most impacted biomes (MEA 2005).

As a consequence, in order to prevent further species and ecosystem losses, most governments have agreed to halve the rate of loss of forests by 2020. Additionally, minimum 17% of terrestrial and inland water systems and minimum 10% of coastal and marine areas are expected to be protected by 2020, especially in areas with high biodiversity and ecosystem service values (CBD 2011). However, ignoring the relationships with other global systems, including energy and food production systems, could undermine biodiversity conservation efforts.

4. Biofuel production for replacing fossil fuels

Biofuel production involves the transformation of organic compounds from living organisms into solid, liquid, or gaseous energy-rich carriers that can be used for energy generation (Kamm and Kamm 2004). Liquid biofuels are mainly produced as bioethanol, used as a substitute for gasoline or as a precursor for the production of ethyl tertiary butyl ether (ETBE) for gasoline blends, and as biodiesel, used as a substitute for diesel (IEA 2016, REN21 2016). For the production of liquid biofuels, organic compounds (e.g., cellulose, hemicellulose, lignin, starch, saccharose, oils, and fats) are transformed into liquid energy carriers (e.g., alcohol and esters). These liquid biofuels are used for offsetting fossil fuels, mainly within the transport sector (Fulton et al. 2015).

Organic compounds can come from different sources (i.e., feedstocks), including herbs, woody plants, oilseeds, agricultural and forestry wastes, and algae (McKendry 2002, Naik et al. 2010). Based on feedstocks, biofuels can be classified into first, second, and third generation biofuels (Brennan and Owende 2010, Naik et al. 2010):

- First generation biofuels are derived from starch, sugar, and oils found in food crops (e.g., maize, wheat, sugarcane, soybean). Fermentation processing technologies are used for ethanol production, while oil extraction and transesterification processing technologies are used for biodiesel production (Naik et al. 2010).

- Second generation biofuels are based in the transformation of lignin and cellulose, which are abundant and common components of non-food plants and organic wastes. (Naik et al. 2010).

- Third generation biofuels are based on the use of microalgae (Lü et al. 2011). Along with second generation biofuels, they have been considered a better alternative for reducing the ecological footprint of biofuel production (Chisti 2008, Demirbas 2010).

4.1 Biofuel from microalgae

Microalgae have been proposed as a more sustainable feedstock for biofuel production (Chisti 2008, Schenk et al. 2008, Brennan and Owende 2010). Biofuel can be produced from prokaryotic (i.e., cyanobacteria) and eukaryotic microalgae (e.g., green algae, red algae, and diatoms), in the forms of biogas, bioethanol, biodiesel, and biohydrogen (Chisti 2007, Schenk et al. 2008, Harun et al. 2009, Brennan and Owende 2010).

Benefits of microalgae cropping include their high yield potential, their ability to grow in a wide range of environmental conditions (e.g., freshwater, brackish water, seawater) and their potential to be produced in non-arable lands. Furthermore, they can be coupled with wastewater treatments and industrial CO_2 sources, helping in water remediation and greenhouse gasses consumption (Chisti 2007, Schenk et al. 2008, Pittman et al. 2011). Additionally, microalgal systems can produce biochar, helping in CO_2 sequestration (Heilmann et al. 2010), as well as products for human consumption and animal feed (Pulz and Gross 2004, Brennan and Owende 2010).

4.1.1 Algae biofuel production process

Growing

Algae growth requires carbon dioxide, light, and a growing medium with inorganic salts (i.e., water with nutrients such as nitrogen, phosphorus, iron and sometimes silicon). Maximum productivities are achieved at high light intensities, constant temperatures (usually between 20 and 35 °C), and optimal pH. Production increases when feeding with CO_2 (Chisti 2007, Lundquist et al. 2010), pathogens are controlled (Mata et al. 2010), and when cell densities and light interception are optimized (Schenk et al. 2008, Bechet et al. 2014).

Outdoor systems include open ponds and closed photobioreactors. Raceway ponds are the most widely used type of open ponds, and consist on a closed recirculation channel, built in concrete or with plastic covering the earth, usually with a depth between 15 and 30 cm, in which algae and growth medium are mixed by paddlewheels at a velocity of at least 15 cm s^{-1} (Chisti 2007, Schenk et al. 2008, Brennan and Owende 2010, Mata et al. 2010). Algae concentrations are low, typically at around 0.05% solids, CO_2 should be added to the water for maximal productivity, and temperature is not controlled, although water evaporation helps to cool the medium (Chisti 2007). Compared to photobioreactors, this system experiences higher water losses through evaporation, is less efficient in CO_2 uptake, and is more prone to contamination by other microorganisms, which results in reduced yields (Chisti 2007, Brennan and Owende 2010). However, to date, they are considered the most cost-effective microalgal production system (Slade and Bauen 2013).

Photobioreactors consist of a series of plates, tubes, bags, columns or domes set in particular arrangements that maximize sunlight uptake. Algae concentrations are higher compared to open ponds, light intensity can be better optimized, temperature can be controlled (though energy or water use increase), and CO_2 can be injected at several intervals in order to ensure continuous carbon uptake, leading to biomass yields up to 5 times the obtained in open ponds (Chisti 2007, Schenk et al. 2008, Lundquist et al. 2010, Chen et al. 2011). However, an excess of oxygen produced by photosynthesis can inhibit algae growth inside the structures, especially at high light intensities and temperatures, and thus a degassing zone should be used to extract oxygen (Chisti 2007). Additionally, capital costs may be ten times higher than those necessary for the construction of open ponds (Schenk et al. 2008), and they have been considered economically unviable by several studies (Lundquist et al. 2010, Davis et al. 2011, Slade and Bauen 2013).

Hybrid systems are based on the initial growth of microalgae in photobioreactors, avoiding contamination by other microorganisms, followed by their growing in open ponds in nutrient limitation conditions, which induces accumulation of lipids and other cellular compounds (Schenk et al. 2008, Pienkos and Darzins 2009).

Harvesting of microalgae, lipid extraction, and biofuel production

Algae can be harvested continuously (chemostat) or every several days (batch mode, e.g., every 2–10 days) (Schenk et al. 2008). Biomass can be recovered from the broth using filtration, absorption, centrifugation, micro screens, flocculation, or sedimentation following changes in pH (Chisti 2007, Darzins et al. 2010, Lundquist et al. 2010). However, this can be a costly practice as a result of the small size of algae and their low specific gravity (Uduman et al. 2010, Wiley et al. 2011, Milledge and Heaven 2013).

For biodiesel production, oils are mainly extracted using solvents (e.g., hexane), although squeezing of cells and solvent-free methods can be used (e.g., supercritical fluid extraction, heated oil extraction, and biological extraction) (Darzins et al. 2010, Ranjith Kumar et al. 2015). Finally, lipids are converted into biodiesel by transesterification chemical reactions, although different technologies, including catalytic hydroprocessing, are being developed (Darzins et al. 2010, Scott et al. 2010).

Ethanol can be produced through microalgae fermentation, using yeasts on microalgae after lipid extraction processes, and by enhancing the extraction of complex carbohydrates from cell walls through different pre-treatments, including the use of acids or alkalis at high temperatures (Harun and Danquah 2011). Biogas can also be produced after the extraction of lipids or on raw microalgae, via anaerobic fermentation, allowing the recycling of nutrients when re-using the waste effluent (Mussgnug et al. 2010, Collet et al. 2011, Prajapati et al. 2014, González-González et al. 2018)

Chapter 1. Contribution to the authorship

I was in charge of the conception and design of the project; acquisition, analysis, and interpretation of the research data; drafting, analysis, and critical writing of the manuscript; and sending of the manuscript to peer-reviewed journals (i.e., as corresponding author).

CHAPTER 1. Biodiversity impacts of bioenergy production: Microalgae vs. first generation biofuels

Diego F. Correa[1, 2*], Hawthorne L. Beyer[2], Hugh P. Possingham[2], Skye R. Thomas-Hall[1], Peer M. Schenk[1]

[1]Algae Biotechnology Laboratory, School of Agriculture and Food Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia

[2] ARC Centre of Excellence for Environmental Decisions, The University of Queensland, Brisbane, Queensland 4072, Australia

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ABSTRACT

Energy and fuel demands, which are currently met primarily using fossil fuels, are expected to increase substantially in the coming decades. Burning fossil fuels results in the increase of net atmospheric CO_2 and climate change, hence there is widespread interest in identifying sustainable alternative fuel sources. Biofuels are one such alternative involving the production of different fuels which include biodiesel and bioethanol from plants. However, the environmental impacts of biofuels are not well understood. First generation biofuels (i.e., biofuels derived from edible biomass including crops such as maize and sugarcane) require extensive agricultural areas to produce sufficient quantities to replace fossil fuels, resulting in competition with food production, increased land clearing and pollution associated with agricultural production and harvesting. Microalgal production systems are a promising alternative that suffers from fewer environmental impacts. Here, we evaluate the potential impacts of microalgal production systems on biodiversity compared to first generation biofuels, through a review of studies and a comparison of environmental pressures that directly or indirectly impact biodiversity. We also compare the cultivation area required to meet gasoline and distillate fuel oil demands globally, accounting for spatial variation in productivity and energy consumption. We conclude that microalgal systems exert fewer pressures on biodiversity per unit of fuel generated compared to first generation biofuels, mainly because of reductions in direct and indirect land-use change, water consumption if water is recycled, and no application of pesticides.

Further improvements of technologies and production methods, including optimization of productivities per unit area, colocation with wastewater systems and industrial CO_2 sources, nutrient and water recycling and use of co-products for internal energy generation, would further increase CO_2 savings. Overall pollution reductions can be achieved through increased energy efficiencies, along with nutrient and water recycling. Microalgal systems provide strong potential for meeting global energy demand sustainably.

Keywords: Biofuel crops, ecological footprint, land-use change, life-cycle assessment, tropic, vertebrate

1. INTRODUCTION

Future energy demands are expected to increase as a result of the ongoing population and economic growth. According to the IEA (2014), energy consumption could increase between 17% and 50% by 2040 relative to 2012, reaching around 15,629 and 20,039 Million Tonnes of Oil Equivalent (MTOE) respectively. Meeting these demands under current levels of fossil fuels exploitation—with coal, oil and gas accounting for 82% of total primary energy consumption in 2012—is likely to drive increases in global atmospheric temperature above 3.6°C by 2100 in comparison to pre-industrial levels (IEA 2014), leading to widespread changes in ecological communities and increases in extinction risks for species (Thomas et al. 2004, Bellard et al. 2012)

Although a system that combines energy derived from the wind, water and sunlight has been proposed for supplying global energy demands (Jacobson and Delucchi 2011), fuels with their high energy density will still be a major component in the future to power large machinery, planes, and ships. Biofuels, defined as high-density energy carriers derived from biomass transformation, could be a sustainable alternative to replace fossil fuels (Goldemberg 2006, Hill et al. 2006, Panwar et al. 2011), especially for the transport sector (IEA 2014, Williams et al. 2015), which in 2012 accounted for around 23% of total CO_2 emissions (IEA 2014). Burning biofuel releases carbon that has been already fixed by plants through photosynthesis and thus, in theory, should not increase the net atmospheric CO_2 content (McKendry 2002, Naik et al. 2010). However, there are concerns about the environmental impacts that a widespread adoption of biofuels could exert at a global scale, which could lead to further environmental degradation depending on the production system and initial land-use (Tilman et al. 2009, Immerzeel et al. 2014). Furthermore, environmental impacts are a function of differences in energy demands per country and regional variation in biofuels' productivities.

Currently, biofuels are primarily produced in the forms of bioethanol and biodiesel derived from food crops (i.e., first generation biofuels). It is estimated that between 2013 and 2015 around 77% of produced bioethanol was based on the processing of maize and sugarcane; while around 81% of biodiesel was produced from vegetable oils (OECD/FAO 2016). Because first generation biofuels compete with agricultural lands, environmental degradation—including biodiversity losses due to land clearing of biodiverse systems—has been associated with biofuels' expansion (Danielsen et al. 2009, Fargione et al. 2009, Fargione et al. 2010, Fletcher et al. 2011, Koh et al. 2011, Duke et al. 2013, Immerzeel et al. 2014). Furthermore, biofuel production can increase the magnitude of other pressures that directly or indirectly affect biodiversity, including CO_2 emissions from land-use change (Fargione et al. 2008, Searchinger et al. 2008, Searchinger et al. 2015) and production systems (Larson 2006, Crutzen et al. 2008, Cherubini et al. 2009), emission of pollutants (Hill et al. 2006, Fargione et al. 2010) and depletion of water (Dominguez-Faus et al. 2009, Gerbens-Leenes et al. 2009, Gerbens-Leenes et al. 2012).

Microalgal production systems, which include open ponds and closed photobioreactors (Chisti 2007, Schenk et al. 2008, Lundquist et al. 2010, Mata et al. 2010, Wijffels and Barbosa 2010) could overcome several drawbacks of first generation biofuels, because they offer higher biomass yields than terrestrial crops per unit area, can be grown on non-arable lands, can make use of brackish or seawater, and can be coupled with wastewater systems and industrial CO_2 sources, helping in water remediation and in CO_2 emission reductions (Chisti 2007, Chisti 2008, Schenk et al. 2008, Brennan and Owende 2010, Mata et al. 2010, Sayre 2010). Previous work on microalgal production systems has addressed several environmental impacts of microalgal biofuel production, including resource consumption and pollution (Lardon et al. 2009, Clarens et al. 2010, Campbell et al. 2011, Clarens et al. 2011, Collet et al. 2011, Slade and Bauen 2013), water consumption (Zaimes and Khanna 2013) and potential impacts of genetically modified strains (Menetrez 2012). However, no study has focused on biodiversity or compared the potential impacts of microalgal systems on biodiversity in relation to first generation biofuels.

Here, we review the potential impacts of microalgal systems for biofuel production on biodiversity in contrast to first generation biofuels, focusing on vertebrates in tropical and subtropical biodiverse regions of the world (Dirzo and Raven 2003, Kier et al. 2005) where the potential for agricultural expansion, including first generation biofuels, is greatest (Laurance et al. 2014, Laurance 2015). We classify the different factors that affect biodiversity due to biofuel production, using the DPSIR framework which, based on Driving forces, Pressures, States, Impacts and Responses, is useful for describing the interactions between society and the environment (Smeets and Weterings 1999, Kristensen 2004). Then, we identify and compare the different pressures—defined as anthropogenic factors that induce environmental impacts (Gabrielsen and Bosch 2003)—that directly and indirectly impact biodiversity, when using microalgal systems or first generation biofuels. Accounting for spatial variation in productivity and energy consumption, we estimate the cultivation area required to meet gasoline and distillate fuel oil for each country using either microalgal systems or first generation biofuels, to investigate the relative impacts of these biofuel production alternatives in terms of potential land-use changes.

2. MATERIALS AND METHODS

Relevant literature was identified in April 2016 using the Science Citation Index Expanded (SCI-EXPANDED) and the Emerging Sources Citation Index (ESCI) in Web of Science, with the following combinations of keywords: (biofuel OR bioenergy) AND (biodiversity OR wildlife), (biofuel OR bioenergy) AND (fish* OR bird* OR avian OR mammal* OR reptil* OR amphibian*). A citation report was made using Web of Science in order to show the progress in the field. Papers were screened to identify those that relate first generation biofuels or microalgae with impacts in tropical and subtropical areas of the world (i.e., between parallels 38°N and 38°S). We used these studies to identify the impacts that biofuel production has on biodiversity, the anthropogenic factors that induce impacts on biodiversity (i.e., pressures), as well as the mechanisms and processes by which those impacts occur.

Further comparisons between microalgal systems and first generation biofuels were based on pressures that directly or indirectly have shown to impact biodiversity. Environmental pressures were schematized based on the DPSIR causal framework (Smeets and Weterings 1999, Kristensen 2004). The DPSIR framework has been adopted by the European Environmental Agency (Smeets and Weterings 1999) and has been widely applied for understanding relationships between factors that drive impacts on the environment and society responses (Immerzeel et al. 2014), for allowing communication between scientists (Maxim et al. 2009) as well as a tool for decision making (Atkins et al. 2011). For this comparison, life-cycle assessments for microalgal production systems were reviewed.

An estimate of the cultivation area required by microalgal systems and first generation biofuels and microalgal systems to meet each country's 2010 gasoline and distillate fuel oil demands (U.S. Energy

Information Administration 2016) was developed. The average yield of crops that could be used for ethanol and biodiesel production between 2005 and 2014 was calculated using the “FAOSTAT” database (FAO 2019) for each country. For each crop, yields can differ among countries located in the same climatic conditions (e.g., same latitude), as a result of differences in cultivars, soils, management practices, age of crops, and other factors that affect production. This can lead to larger land footprints in countries with less efficient agricultural practices, based on the same crop and similar gasoline and distillate fuel oil demands. Average ethanol yields were then estimated using conversion efficiencies from feedstocks (Wang et al. 1997, Rajagopal et al. 2007, de Vries et al. 2010, El Bassam 2010) and average biodiesel yields were estimated using reported lipid contents and oil-specific densities per crop (El Bassam 2010, Firestone 2013), assuming lipid extraction efficiencies of 90% and lipid conversion efficiencies of 90%. For microalgal systems, lipid yields were obtained using the global map developed by Moody et al. (2014). The most frequent value of lipid yield per country was obtained based on an area-weighted average. The total cultivation area required to meet each country’s gasoline and distillate fuel oil needs was then calculated by dividing their annual consumption in 2010 (GJ year^{-1}) by the average biofuel yield per country (GJ ha^{-1} year^{-1}) (see Supplementary Information for details about calculations).

3. RESULTS AND DISCUSSION

We identified 898 papers addressing the impacts of biofuels on biodiversity, 101 of which related first generation biofuels or microalgal systems to biodiversity in tropical and subtropical regions of the world. From this only three studies focused specifically on microalgal systems (Zhu and Ketola 2012, Usher et al. 2014, Zhu et al. 2015) (Tables S1 and S2 in Supplementary Information). A citation report generated in Web of Science shows the increasing trend in the number of citations for recent years, from five citations in 1993 to 5036 citations in 2015 and 4243 citations in 2016 (Fig. 1).

Increases in population growth, energy and food demands, and replacement of fossil fuels were identified as the main drivers for biodiversity changes arising from biofuel expansion. A wide range of pressures that affect biodiversity were identified (Fig. 2). Because first generation biofuels make use of food crops, the pressures that impact biodiversity are closely related to those found for agricultural systems (McLaughlin and Mineau 1995, Donald 2004). These pressures corresponded to changes in land-use, overexploitation of resources, pollution, and changes in environmental conditions that directly or indirectly impact biodiversity: land-use change (direct, indirect) and land-use intensification, increases in greenhouse gas emissions (leading to global warming), pesticide and fertilizer pollution, water depletion, overexploitation of soils (including soil erosion), increases in invasive species and genetic pollution, emissions of air pollutants and changes in environmental conditions that affect regional climate.

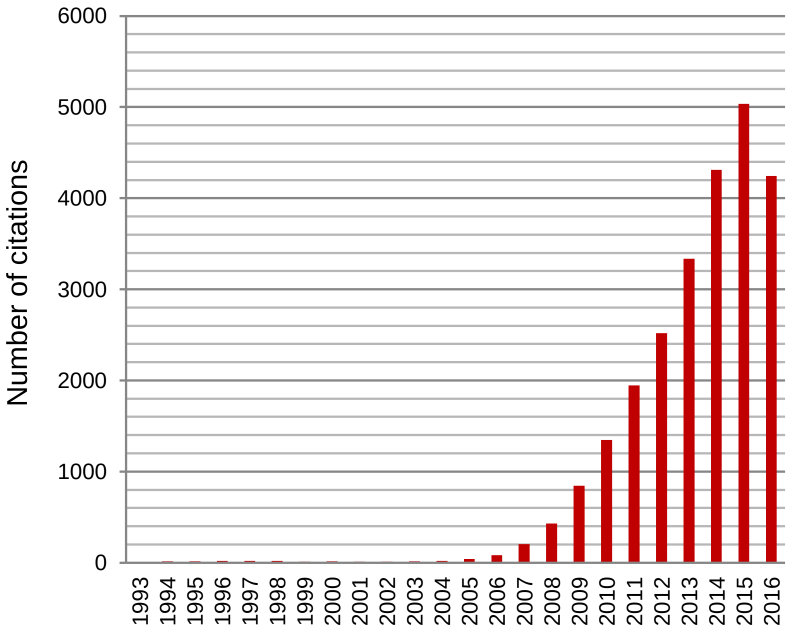

Figure 1. Citation report using the Science Citation Index Expanded (SCI-EXPANDED) and the Emerging Sources Citation Index (ESCI) in Web of Science and the following combination of keywords: (biofuel OR bioenergy) AND (biodiversity OR wildlife), (biofuel OR bioenergy) AND (fish OR bird* OR avian OR mammal* OR reptil* OR amphibian*).*

These pressures alter the state of ecosystems, resulting in a series of impacts on biodiversity (Fig. 2). Responses of society to these impacts may increase or decrease their magnitude. For instance, adaptation measures to climate change may drive further environmental degradation without adequate planning for biodiversity conservation (Watson 2014, Maxwell et al. 2015), which outlines the importance of defining priorities that satisfy societal needs at the minimum costs for biodiversity (Balvanera et al. 2001).

These pressures can directly or indirectly impact biodiversity through several mechanisms. For instance, land-use change directly decreases available habitat, but can also lead to fragmentation that further increases potential extinction risks in the remaining habitat patches (Fahrig 2003, Krauss et al. 2010). Furthermore, the magnitude of biodiversity impacts resulting from biofuel crop expansion was found to be a function of initial land-use, type of biofuel system and its associated management practices and production technologies, and landscape configurations between biofuel crops and native ecosystems (Azhar et al. 2011, Immerzeel et al. 2014). We examine each category of pressure in detail in the following sections.

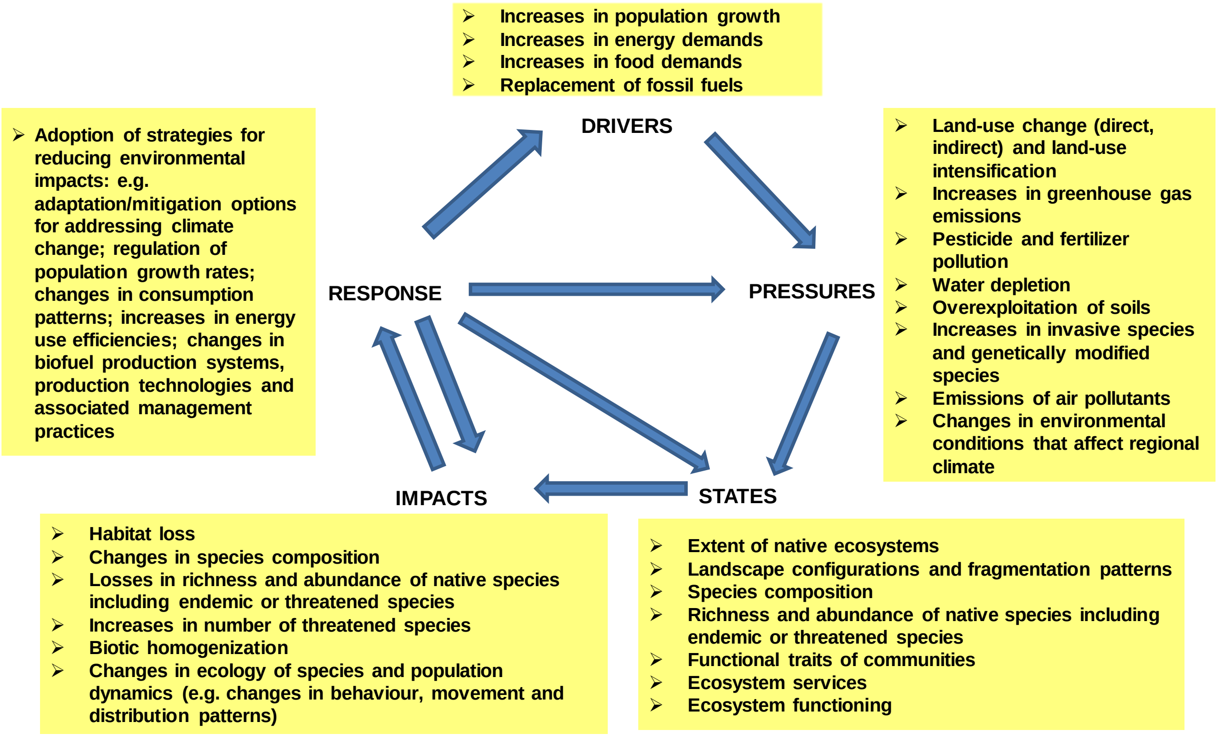

Figure 2. Drivers, Pressures, States, Impacts, and Responses of biofuel production on biodiversity, based on the reviewed literature and following the DPSIR framework.

3.1 Direct land-use change and land-use intensification

Land-use change and land-use intensification were reported as the main pressures negatively impacting biodiversity due to the expansion of first generation biofuel systems (Immerzeel et al. 2014, Savilaakso et al. 2014). Replacement of native ecosystems and cropping intensification have been linked to habitat loss and degradation, decreases in richness and abundance of native vertebrates, affecting species of high conservation concern (Buchanan et al. 2008, Alkemade et al. 2009, Carrete et al. 2009, Meehan et al. 2010, Fletcher et al. 2011, Immerzeel et al. 2014). Furthermore, species that make use of biofuel plantations are mostly considered generalists and of low conservation value (Rajaratnam et al. 2007, Fitzherbert et al. 2008, Koh and Wilcove 2008, Danielsen et al. 2009, Azhar et al. 2011, Codesido et al. 2011, Fletcher et al. 2011, Mahood et al. 2012, Savilaakso et al. 2014, Pardo et al. 2015).

Impacts on biodiversity depended upon the initial land-use, the type of biofuel production system and the landscape configuration. Reductions of species diversity are larger when transforming very biodiverse ecosystems (Duke et al. 2013) such as tropical forests (Koh and Wilcove 2008, Laurance

2015) and savannas (Alkemade et al. 2009, Searchinger et al. 2015) and when using biofuel production systems that require a larger area per unit of energy produced (Geyer et al. 2010). In some circumstances, where biofuel crops recreate ecological conditions needed for the survival of native species, vertebrate diversity could increase. For instance, it has been proposed that the replacement of degraded lands by several biofuel crops could increase biodiversity values. In the Indonesian tropics, if degraded *Imperata* grasslands are replaced with oil palm plantations, which are structurally and functionally more complex than pastures, diversity of forest-dependent vertebrates is expected to increase (Fitzherbert et al. 2008)—though mostly for low conservation value species—and lead to less pressure on forests (Nantha and Tisdell 2009). In the USA, large patches of perennial crops (e.g., switchgrass, *Miscanthus*, mixed-grass prairies) are expected to be better than annual crops (e.g., maize) for maintaining populations of grassland specialists including endangered vertebrates (e.g., the Henslow's sparrow), provided that management practices (e.g., application of pesticides and harvesting) do not negatively affect the fitness of species (Fargione et al. 2009, Fletcher et al. 2011, Robertson et al. 2011).

If large patches of forests remain near to biofuel plantations, several forest species can use oil palm plantations, even endangered vertebrates. For instance, it has been shown that chimpanzees can make use of oil palm plantations, eating young leaves, flowers, and fruits when other sources of food are scarce (Wich et al. 2014). Populations of large and medium-sized felids can make use of oil palm plantations if native forest tracts remain (Pardo et al. 2015). However, the benefits may be diminished by negative interactions between humans and wildlife where species are perceived as pests, or where they are systematically hunted (Peres 2000, Michalski et al. 2006, Treves et al. 2006).

Microalgal cultivation systems need less land than first generation biofuels in order to produce the same amount of energy, and thus it is expected that their widespread adoption would lead to less direct land-use changes and lower relative habitat losses for native species. However, estimates for lipid productivities are very wide, ranging between 2.3 and 136.9 kL ha^{-1} year^{-1} (Quinn and Davis 2015). Thus, we compare potential land savings based on a more conservative worldwide lipid estimation developed by Moody et al. (2014), which closely resembles calculated productivities in experimental outdoor raceway ponds (Schenk 2016).

Based on regional changes in productivity for food crops and microalgae (See Materials and Methods for details), our calculations show that microalgal cultivation systems consistently need less land than the most productive first generation biofuel crop per country (Fig. 3). For instance, in order to meet the USA gasoline and distillate fuel oil demands, microalgal systems would need 23.7% the area needed by olives and 40.8% the area needed by sugar beets cropped within the country (Tables S5 and S6 in Supplementary Information). This is an optimistic scenario for first generation biofuels because yields are based on areas where crops grow well, and it is assumed that these crops can be readily used for biofuel production. For microalgal systems, conservative yields are assumed, based on the area-weighted average of average lipid yields within each country based on the Moody et al. (2014) global estimates.

Furthermore, microalgae can be grown in areas not suitable for other crops (i.e., in poor soils and in regions with low precipitation values) (Schenk et al. 2008, Mata et al. 2010). If microalgal production proves to be feasible in these areas, less land-use change and intensification in highly biodiverse regions is expected, although marginal or degraded lands can still retain considerable biodiversity values (Meehan et al. 2010, Plieninger and Gaertner 2011), and the construction of microalgal facilities will inevitably decrease available habitat for native species (Zhu et al. 2015).

3.2 Indirect land-use change

Leakage effects result when economic activities are displaced into different regions where biofuels are grown (Cottier et al. 2009). Indirect land-use change occurs when agricultural lands displace into regions previously occupied by native ecosystems or non-intensive production systems including extensive pastures and agroforestry systems (Edwards et al. 2010, Fargione et al. 2010, Lapola et al. 2010, Alexandratos and Bruinsma 2012, Castanheira et al. 2014). For example, the European Union biofuel policies are expected to lead to increased land-use changes outside Europe and transfer environmental impacts to more biodiverse regions (Schleupner and Schneider 2010, Frank et al. 2013, Pelikan et al. 2015). Biofuel cropping has also been related to indirect land-use change as a result of complex interactions between economic factors, including increases in food prices and economic incentives for biofuel production (Mitchell 2008, Lambin and Meyfroidt 2011, Zilberman et al. 2013).

Infrastructure development associated with agricultural expansion can further drive land-use changes, as shown in tropical remote regions, where deforestation increases due to higher accessibility and cropping profitability when roads are constructed or paved (Soares-Filho et al. 2006, Laurance et al. 2014). In fact, oil palm and soybean expansion are related to road expansion and further deforestation in Southeast Asia and South America (Fitzherbert et al. 2008, Lee et al. 2011). For instance, in the Brazilian Cerrado, increased accessibility to forests around soybean plantations has led to further deforestation for fueling the steel industry, which not only decreases the area of remaining forests but also generates profits for further soybean expansion (Casson 2003, Lee et al. 2011).

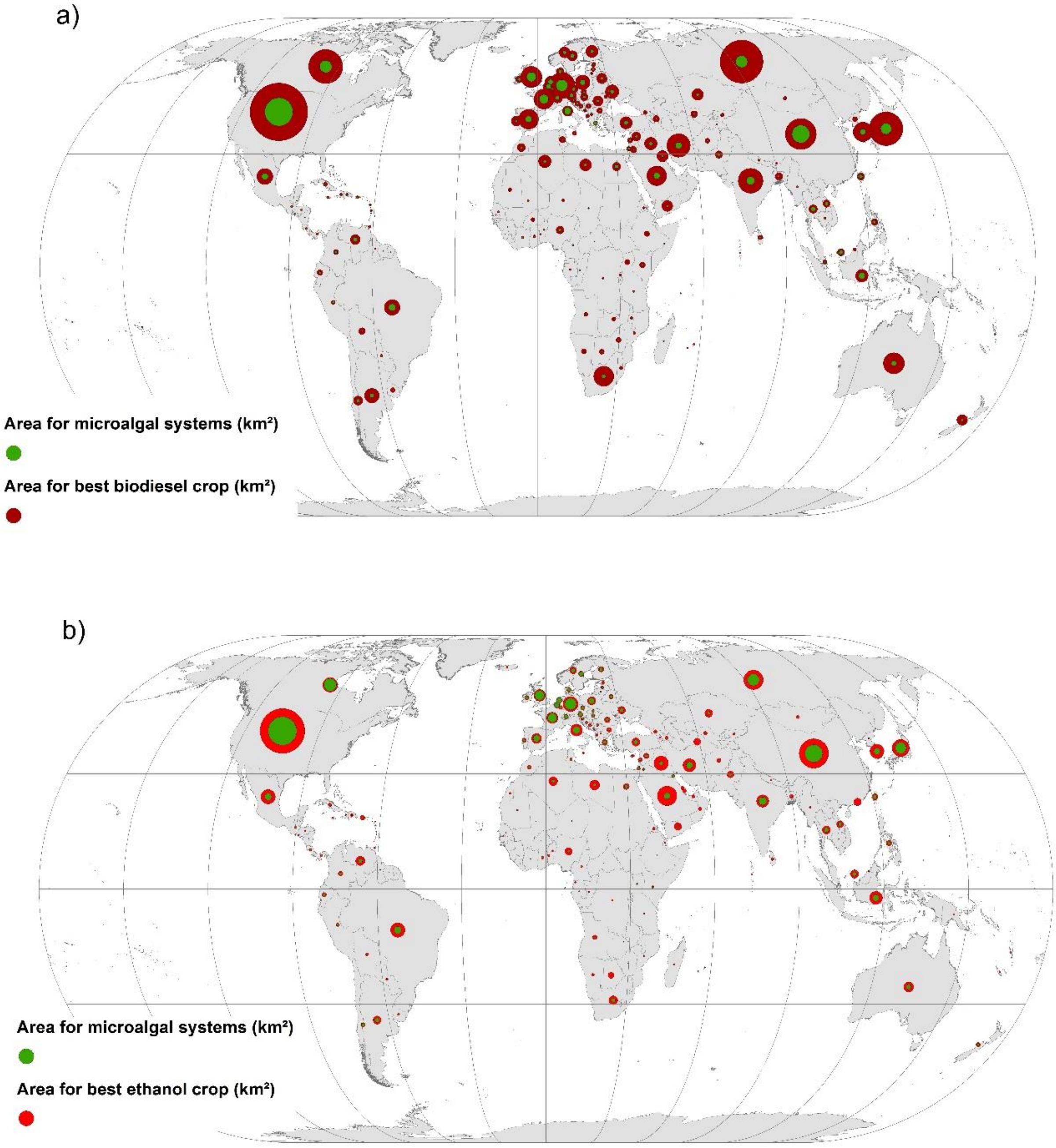

Figure 3. Superimposed circles showing the cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, when comparing microalgal systems with the most productive biodiesel and bioethanol crop per country.For first generation biofuels, yields are based on areas where crops possibly grow best (average yields between 2005 and 2014) (FAO 2019), while the most frequent value (area-weighted average) of average lipid yield within countries is used for microalgal systems. Microalgal lipid estimations are based on Moody et al. (2014).

Microalgal systems are not considered to drive indirect land-use changes (Fritsche et al. 2010). This is because if they are produced in degraded, dry or marginal lands that are less suitable for food production, less competition with agricultural lands would occur, which is expected to lead to fewer leakage effects, land clearing, and transformation of biodiverse systems. This assumption is contingent upon the feasibility of microalgal biofuel production in areas not suitable for agricultural production. However, economic activities currently developed in degraded, dry, or marginal lands (e.g., grazing and mining) could be displaced into agricultural areas and biodiverse regions as a result of microalgal production. Further analyses that consider how microalgal biofuel production would reduce pressures on more humid areas (which include lands of higher agricultural and biodiversity value), while increasing pressures on dry areas (e.g., through the development of roads, construction of infrastructure, and population growth), would be required.

3.3 Increases in greenhouse gas emissions

Biofuel expansion affects the emission of greenhouse gasses via land-use change and energy-intensive production systems (Creutzig et al. 2015), while co-products can help in decreasing greenhouse gas emissions. These emissions of greenhouse gasses have been linked to local extinction and habitat shifts for native species through global warming (Thomas et al. 2004, Bellard et al. 2012).

3.3.1 Greenhouse gas emissions as a result of land-use change

The clearing of carbon-rich systems releases CO_2 when plant biomass is burnt and soil organic carbon is lost (Fearnside 2000, Guo and Gifford 2002, Don et al. 2012). In Brazil, it would take around 17 years to recapture the CO_2 emmited after native grasslands are replaced by sugarcane crops (Fargione et al. 2008). In Indonesia, around 423 years would be needed to recapture the CO_2 emmited after peatland rainforests are replaced by oil palm plantations (Fargione et al. 2008). Based on satellite images, Koh et al. (2011) estimated that between 2000 and 2010 the conversion of forests into oil palm plantations in Malaysia, Borneo, and Sumatra led to the loss of around 140 million Mg of aboveground biomass carbon. Furthermore, first generation biofuel production can lead to indirect land-use changes, which would further drive the clearing of native ecosystems for crop production, and thus increase greenhouse emissions (Searchinger et al. 2008).

Initial land-use is expected to alter the magnitude of CO_2 emissions as a result of microalgal biofuel production (Stephenson et al. 2010). Because microalgal production systems need less land for producing the same amount of energy than terrestrial crops, and their production can be achieved in places with naturally lower carbon stocks (i.e., degraded and dry areas), it would be expected that much less CO_2 would be released following direct land-use changes when using microalgal systems compared to first generation biofuels. If degraded areas, dry areas, and marginal lands are used for microalgal biofuel production, or even for the production of microalgal animal feed, less competition with crops is expected to occur, leading to less indirect land-use changes and lower CO_2 emissions. In fact, it has been estimated that the global expansion of microalgae as a feedstock for animal feed, in areas not suitable for agricultural production, could free almost 2 billion hectares of pastures and feed crops, where forest plantations can be established for bioenergy production and habitat restoration, leading to net atmospheric CO_2 reductions (Walsh et al. 2015). However, if carbon-rich systems are used for microalgal production, CO_2 emissions may become substantial. For instance, Quiroz-Arita et al. (2016) estimate that within the USA the CO_2 savings of microalgal systems may decrease between 3% and 85% as a result of losses in aboveground biomass and soil carbon associated to land-use changes.

3.3.2 Production technologies and greenhouse gas emissions

Biofuel production systems and their associated cropping management practices and conversion technologies affect the balance of greenhouse gas emissions (Creutzig et al. 2015). In agriculture, greenhouse gas emissions come from energy consumed along the production chain (CO_2 emissions), fertilizer use (liberation of N_2O and CO_2), cultivation in flooding conditions (CH_4 emissions) and soil management practices including tillage, the addition of lime, and irrigation frequency (Snyder et al. 2009).

As a result, crops with lower fertilizer requirements, coupled with management practices that optimize nutrient uptake and soil carbon storage, and less energy-intensive production technologies, would lead to lower greenhouse gas emissions. For instance, in the USA biodiesel production from soybeans captures more greenhouse gasses than bioethanol production from maize (41% vs. 12% respectively; taking into account the energy used for crop cultivation, biofuel production and transport), mainly because of lower agricultural inputs and less intensive processes for biofuel production (Hill et al. 2006).

In comparison to terrestrial crops, microalgal systems can offer higher CO_2 savings when using efficient technologies under optimal production conditions (Liu et al. 2012). However, a consensus in optimal production technologies—that maximizes both cost-effectiveness and reductions in CO_2 emissions—has not been reached. This is because large commercial microalgal farms for biofuel production have not been deployed, and because of difficulties in comparing studies that have different system boundaries, sources of electrical energy, functional units, influence of co-products and model parameters (Handler et al. 2012, Liu et al. 2012, Quinn and Davis 2015) (Table 1).

Open raceway ponds are estimated to be energetically more efficient than photobioreactors (Resurreccion et al. 2012, Slade and Bauen 2013), leading to higher CO_2 savings (Kendall and Yuan 2013). Using open ponds, carbon savings can further increase due to higher productivities per unit area (Stephenson et al. 2010, Campbell et al. 2011, Xu et al. 2011, Sills et al. 2012), colocation of microalgal systems with CO_2 sources (e.g., use of flue gas) (Clarens et al. 2010, Sander and Murthy 2010, Campbell et al. 2011, Clarens et al. 2011, Shirvani et al. 2011, Zaimes and Khanna 2013) or wastewater systems (Clarens et al. 2010, Clarens et al. 2011), and use of technologies that allow nutrient recycling (e.g., water recycling) (Sander and Murthy 2010, Kendall and Yuan 2013, Zaimes and Khanna 2013) and production of energy (e.g., anaerobic digestion for producing methane which can be used for electricity generation) (Collet et al. 2011, Hou et al. 2011, Resurreccion et al. 2012, Sills et al. 2012, Grierson et al. 2013, Quinn et al. 2014, Quinn and Davis 2015). However, Clarens et al. (2011) suggest that anaerobic digestion for nutrient recycling and energy production is not the best approach for reducing greenhouse gas emissions compared to the direct combustion of algal biomass, although increases in digestibility, methane production, and nutrient recovery could increase the environmental benefits of this technology.

Increasing the energy efficiency of production methods is also important for reducing emissions, such as through improved water pumping methods and more efficient lipid extraction processes (Xu et al. 2011, Slade and Bauen 2013). In fact, wet extraction routes have the potential for decreasing energy inputs and increase CO_2 savings (Lardon et al. 2009, Sills et al. 2012, Slade and Bauen 2013), especially through hydrothermal liquefaction (Grierson et al. 2013, Bennion et al. 2015). Overall, increasing low-carbon energy sources for microalgal production systems, including heat, electricity grid, fertilizers, transport, and building materials not derived from fossil fuels, would lead to further carbon savings (Shirvani et al. 2011).

Thus, substantially increased carbon savings in comparison to first generation biofuels are feasible. For instance, Lardon et al. (2009) estimated that assuming biomass productivities between 20 and 30 $g\ m^{-2}\ d^{-1}$ for *Chlorella vulgaris* grown in open raceway ponds under Mediterranean conditions, and using wet extraction lipid routes, microalgal production could lead to less global warming potential when compared to soybean and conventional diesel, but not to oil palm or rapeseed. However, this study did not take into account nutrient recycling through anaerobic digestion or culture medium recycling. Stephenson et al. (2010) estimated that the production of *C. vulgaris* in open raceway ponds under U.K. conditions could lead to higher carbon savings than biofuel obtained from soybean, sunflower and rapeseed grown in South Africa or from oil palm in Malaysia; assuming higher lipid productivities, production in degraded lands, use of flue gas from power stations, nutrient recycling, energy production through anaerobic digestion, and lower velocities for microalgal cultivation. Clarens et al. (2011) found that assuming biomass yields of 91.1 Mg ha^{-1} $year^{-1}$ for brackish water species grown in Southwestern USA conditions with lipid contents of 19.6%, greenhouse gas emissions per kilometer traveled would be lower compared to rapeseed.

3.3.3 Influence of co-products in greenhouse gas emissions

Co-products of biofuel production help in increasing CO_2 savings. These include dried distillers grains, feed products, CO_2, starch, syrup, and oils (e.g., corn oil) in the case of bioethanol production from sugar and starch crops, as well as protein meal and glycerol from biodiesel production (Naik et al. 2010). Microalgal systems can be designed to produce not only biodiesel or bioethanol as main biofuel products but also a wide arrange of co-products that can be used for energy production, food and animal feed (Brennan and Owende 2010, Wijffels et al. 2010). For instance, using wet conversion routes it is possible to produce biodiesel, carbon monoxide, hydrogen, methane, ethane, and propane, while through dry conversion, biodiesel, glycerol, pyrolysis oil, and biogas can be produced (Gerbens-Leenes et al. 2014).

Co-products are considered fundamental for increasing the cost-effectiveness and sustainability of microalgal biofuel production systems (Wijffels et al. 2010, Liu et al. 2012). In particular, methane production has been identified as a key co-product that increases carbon savings when it is combusted for replacing external energy requirements (Sialve et al. 2009, Collet et al. 2011, Resurreccion et al. 2012, Sills et al. 2012, Quinn et al. 2014, Quinn and Davis 2015).

Table 1. Comparison between several life-cycle assessments developed to date, in relation to system boundaries, main processing technologies, measured environmental impacts, and main results. Cultivation System (CS). Open raceway pond (OP), photobioreactor (PB), open raceway pond integrated with photobioreactor (OP-PB), Not Stated (N.S.).

Species	CS	System boundaries	Main processing technologies	First gen. biofuels	Measured environmental impacts	Main results	Notes	Reference
Chlorella vulgaris	OP	Cradle-to-combustion analysis for the fuel, cradle-to-grave analysis for the facility. Includes extraction and production of raw materials, facility construction and dismantling, biofuel production and use in the engine.	1) Advanced drying followed by hexane extraction. 2) Direct extraction from the wet algal paste.	Rapeseed, soybean, oil palm	Abiotic depletion, potential acidification, eutrophication, global warming potential, ozone layer depletion, marine toxicity, human toxicity, land competition, emission of ionizing radiation, photochemical oxidation.	Lower land competition and eutrophication compared to first generation biofuels. Lower acidification potential in comparison to rapeseed and lower human toxicity in comparison to rapeseed and oil palm. Lower global warming potential in comparison to soybean. Higher abiotic depletion, ozone layer depletion, marine toxicity, ionizing radiation, and photochemical oxidation compared to first generation biofuels.	Assumed biomass productivities at 20–30 g m^{-2} day^{-1} in Mediterranean conditions. Functional unit as the combustion of 1 MJ of fuel in a diesel engine.	(Lardon et al. 2009)
Chlorella vulgaris	OP	Microalgal cultivation to downstream fuel production. Includes cultivation, harvesting, dewatering, oil extraction, oil upgrading and nutrient recycling.	Harvesting by flocculation and centrifugation, followed by dry conversion routes for lipids (transesterification) or wet conversion routes lipids (hydrogenation).	Several vegetable oils and sugar crops	Land use	Large positive energy balance in comparison to first generation biofuels can be achieved. Potential to increase productivity and decrease nutrient usage by nitrogen deprivation during growing. Larger land savings when increasing the productivity per unit area.	Assumed lipid contents between 19.7–43% and 15% of nutrient recycling for wet processing route.	(Xu et al. 2011)
Chlorella vulgaris	OP	Production, harvesting and concentration of algae, methane extraction and combustion, facility construction and dismantling, extraction and shipping of resources.	Harvesting by settling and centrifugation followed by injection in anaerobic digesters, biogas burning and production, CO_2 reinjection into cultures.	Rapeseed, oil palm	Abiotic depletion, potential acidification, eutrophication, global warming potential, ozone layer depletion, human toxicity, land competition, emission of ionizing radiation, photochemical oxidation.	Lower impacts compared to first generation biofuels for acidification, eutrophication, ozone layer depletion, and photochemical oxidation, when assuming low energy consumption by paddlewheels and pumping water (Clarens et al. 2010). Global warming potential decreases when assuming low energy consumption.	Assumed biomass productivities of 25 g m^{-2} day^{-1} in Mediterranean conditions (Narbonne, France). Low energy consumption of paddlewheels and pumping water is assumed based on Clarens et al. (2010). Functional unit as the combustion of 1 MJ of fuel in an internal combustion engine.	(Collet et al. 2011)
Chlorella vulgaris	OP	Cultivation, harvesting, lipid extraction, fuel distribution and combustion by end users.	Harvesting by flocculation, drying and algae oil extraction.	N.S.	Greenhouse gas emissions.	Higher CO_2 emissions compared to conventional diesel for most scenarios.	Assumed biomass productivities of 75 tonnes ha^{-1} year^{-1} and average algae oil content of 30–70%. Explicit analyses in U.K., France, Brazil, China, Nigeria, and Saudi Arabia. Assumes use of CO_2 from nearby power plants (12.5%). Includes three options for co-product use: co-firing of biomass residues, direct combustion in a biomass/heating system or a biomass combined heat and power unit. The functional unit set as 1 MJ of biodiesel produced from algae oil.	(Shirvani et al. 2011)
Chlorella vulgaris	OP	Cradle-to-gate, including processes upstream of dried biomass production.	Harvesting by centrifugation or chamber filter press followed by two algal drying options (natural gas based drying or waste heat drying).	N.S.	Greenhouse gas emissions, direct water demands.	Greenhouse gas savings for 5 out of 8 scenarios analyzed. Water demands were related to geographic locations and their local evaporation rates.	Assumed algae composition of 20% lipids, 25% carbohydrates and 50% protein at 21 geographic locations in the contiguous USA. Includes colocation with natural gas power plant and water recycling. Functional unit as 1 MJ of dried algal biomass.	(Zaimes and Khanna 2013)

Chlorella vulgaris	OP	Culture, harvest, drying, extraction, and esterification.	Drying and lipid extraction.	Maize, potato, sugarcane, sugar beet, sorghum, soybean	Water footprint, nutrient depletion.	The water footprint is in general lower compared to first generation biofuels, and lowest if recycling water or using wastewater/seawater. Nutrient usage is lower when recycling water and when using wastewater or seawater.	Assumed use of freshwater, seawater, and wastewater in California conditions.	(Yang et al. 2011)
Chlorella vulgaris	OP, PB	Cultivation, harvesting and lipid extraction, anaerobic digestion, oil extraction, esterification, transport of oil and final combustion in vehicles.	Harvesting by flocculation, followed by centrifugation (for open raceway ponds), cell disruption by homogenization, hexane lipid extraction, anaerobic digestion for onsite electricity use.	Rapeseed, sunflower, soybean, oil palm	Global warming potential (CO_2, NO_2, CH_4), water depletion.	Lower global warming potential for open raceway ponds and compared to rapeseed, sunflower and soybean biodiesel grown in arable lands in South Africa and compared to oil palm grown in Malaysia. Higher water requirements for photobioreactors under U.K conditions.	Assumed oil productivities at 40 tonnes ha^{-1} year^{-1} and production in degraded lands in U.K. Assumes nitrogen deprivation, co-product allocation, use of flue gas from power stations (12.5% CO_2). Functional unit as the combustion of 1 tonne of biodiesel in a car engine filled at a U.K. station.	(Stephenson et al. 2010)
N.S.	N.S.	Well-to-wheel. Includes cultivation, processing and biofuel production, transport and final use of biodiesel.	Harvesting, and extraction followed by transesterification and excess methanol recycling.	Soybean	Abiotic depletion potential, global warming potential, ozone depletion potential, photochemical oxidation potential, acidification potential, eutrophication potential, human toxicity potential, freshwater aquatic ecotoxicity potential, marine aquatic ecotoxicity potential, terrestrial ecotoxicity potential.	Lower impacts in comparison to first generation biofuels for most assessed impacts.	Assumed biomass productivities between 5–50 g m^{-2} day^{-1} and lipid contents between 15–80% in China conditions. Includes co-product allocation and analyses for water recycling. Functional unit as 1 MJ of energy from biodiesel well-to-wheel.	(Hou et al. 2011)
N.S.	OP	Cradle-to-gate, including the processes upstream of dry biomass production.	Harvesting through flocculation and centrifugation.	Rapeseed, maize	Water use, greenhouse gas emissions, eutrophication potential, land use.	Higher impacts than first generation biofuels in terms of energy use, greenhouse gas emissions and water use, mainly driven by demand for CO_2 and fertilizer. Lower impacts for land use and eutrophication potential compared to first generation biofuels. Using wastewater leads to CO_2 savings and decreases water footprint.	The model was run for Virginia, Iowa, and California, USA. Included scenarios for colocation with wastewater and industrial CO_2 sources. Functional unit as 317 GJ of biomass-derived energy.	(Clarens et al. 2010)
N.S.	OP-PB	Well-to-pump. From cultivation to biofuel final use at refueling stations.	1) Filtration through chamber filter press followed by drying and hexane extraction. 2) Centrifugation followed by drying and hexane extraction.	Soybean	CO_2 emissions, emissions of air pollutants (VOC, CO, NO_x, particulate matter, SO_x, CH_4).	Higher CO_2 savings in comparison to soybeans when using filter press and co-product allocation. High energy consumption for thermal algae dewatering.	Assumed 30% lipids, 31% carbohydrates and 37.5% proteins. Includes recycling of water and addition of external CO_2 sources. Includes co-product allocations. Functional unit as 1,000 MJ of energy at a refueling station.	(Sander and Murthy 2010)

N.S.	OP-PB	Well-to-wheel. Includes cultivation, harvesting and dewatering, lipid extraction, lipid conversion to a liquid transportation fuel, and co-products from defatted algae.	1) Harvesting by best filter press followed by wet lipid extraction and hydrothermal liquefaction, hydrotreatment for lipid conversion and use of anaerobic digestion or animal feed. 2) Harvesting by centrifugation followed by hexane lipid extraction, lipid conversion by transesterification and use of anaerobic digestion or animal feed.	N.S.	Global warming potential.	Lower global warming potential for wet lipid extraction routes compared to dry extraction and for high productivity scenarios.	Estimated ranges of expected values of life-cycle assessment metrics based on Monte Carlo simulations. Assumed 1210 ha microalgal facility using seawater and three ranges in biomass productivities: low (2.4−16 g m^{-2} day^{-1}), base (17−33 g m^{-2} day^{-1}), and high (34−50 g m^{-2} day^{-1}). Functional unit defined as 1 MJ of liquid biofuel (biodiesel or “green” diesel).	(Sills et al. 2012)
N.S.	OP, PB	Cradle-to-wheel. From upstream of the delivered energy product to consumer use (passenger automobile).	Harvesting by auto-flocculation followed by thickening, homogenization, lipid extraction, solvent recovery and anaerobic digestion, belt-filter pressing, and transesterification for biodiesel production.	N.S.	Climate change (global warming potential from greenhouse gas emissions), net water use, net eutrophication potential.	Open ponds that use brackish water are the preferred option for decreasing global warming potential.	Assumed biomass yields between 41.6–95.7 Mg ha^{-1} year^{-1}, and lipid contents between 13.4–32.4% using freshwater and brackish water species. Assumes use of virgin CO_2 from commercial sources. Includes production of biodiesel and methane-derived bioelectricity.	(Resurreccion et al. 2012)
N.S.	OP, PB	Several system boundaries based on reviewed studies.	Several processing technologies based on reviewed studies.	Sugarcane	CO_2 emissions.	Higher variability in CO_2 emissions in comparison to sugarcane. Emissions decrease when using open raceway ponds and when recycling water.	Reviews different studies that relate CO_2 emissions with production technologies.	(Kendall and Yuan 2013)
N.S.	OP	Cradle-to-grave, excluding the production facilities and its construction	Addition of flocculants for algae concentration followed by heating, centrifugation and lipid extraction using methanol and a catalyst. Anaerobic digestion for electricity generation.	Rapeseed	Greenhouse gas emissions (CO_2, CH_4, NO_2).	Higher CO_2 savings in comparison to rapeseed, highest when assuming high algae productivities and when using CO_2 from an ammonia plant.	Assumed biomass productivities at 15–30 g m^{-2} day^{-1} and use of salt water in Australian conditions. Includes three options for CO_2 feeding: in pure form from an ammonia plant, from flue gas (15% concentration) or delivered by truck in liquefied form. Functional unit as combustion of enough fuel in an articulated truck diesel engine to transport one tonne of freight one kilometer.	(Campbell et al. 2011)
Nannochloropsis salina	OP-PB	Well-to-pump, including microalgal cultivation through the delivery of fuel to the filling station. Well-to-wheel for comparison with conventional diesel.	Harvesting by settling, dissolved air flotation and centrifugation, followed by pressure homogenization, hexane extraction, and nutrient recovery through anaerobic digestion.	N.S.	Greenhouse gas emissions (CO_2, CH_4, NO_2).	Lower CO_2 emissions for the scenario that includes improved algae productivity and anaerobic digestion.	Assumed biomass productivities at 25 g m^{-2} day^{-1} and lipid concentrations between 25–50%. Four scenarios were taken into account: baseline, improved algal productivity, supercritical CO_2 extraction, no nutrient recycling (lipid extracted biomass used as cattle feed). Functional unit as 1MJ of biofuel produced.	(Quinn et al. 2014)

***Nannochloropsis* sp.**	OP-PB	Cradle-to-gate, including microalgal cultivation through biodiesel production.	Dewatering and drying through the use of flocculants and centrifugation followed by hexane extraction and transesterification.	N.S.	CO_2 emissions.	High energy consumption for lipid extraction and biodiesel production. CO_2 savings were not found.	Assumed biomass productivities of 25 g m^{-2} day^{-1} in Singapore conditions and using seawater. Lipid contents between 25–45%. Functional unit as 1 MJ biofuel.	(Khoo et al. 2011)
***Phaeodactylum* sp., *Tetraselmis* sp.**	OP	Well-to-wheel. Includes extraction of raw materials, cultivation and lipid extraction, conversion and use of biofuel in vehicles.	Cultivation followed by harvesting through auto-flocculation, thickening, and homogenization. Several scenarios for biomass processing: 1) Anaerobic digestion of bulk algae biomass for the production of electricity from methane. 2) Production of biodiesel from algae lipids coupled with anaerobic digestion for producing electricity. 3) Production of biodiesel from lipids and direct combustion for electricity production from residual algae biomass. 4) Direct combustion of algae biomass for producing electricity.	Rapeseed, maize	Net energy use, water use, and greenhouse gas emissions.	Highest energy efficiencies when using direct combustion of algae biomass for producing electricity, and lowest when producing biodiesel from algae lipids coupled with anaerobic digestion for producing electricity. Use of wastewater and flue gas increases energy efficiencies. Algae systems are better than rapeseed and maize in relation to vehicle kilometers traveled per ha. Greenhouse gas emissions and water used per kilometer traveled are lower compared to rapeseed	Assumed biomass yields of 91.1 Mg ha^{-1} $year^{-1}$ and lipid contents at 19.6% using brackish water species in Southwestern USA conditions and in marginal lands. Includes scenarios for CO_2 sources: virgin CO_2, carbon capture from coal-fired using chemical sorption, use of flue gas 12.5% CO_2 power plant. Includes one scenario for wastewater use. Makes use of stochastic inputs to capture uncertainty in processes. Functional unit as usable energy production per unit land area (vehicle kilometers traveled per ha) and environmental burdens (net energy use, water use, and greenhouse gas emissions per vehicle kilometers traveled).	(Clarens et al. 2011)
Scenedesmus dimorphus	OP	Well-to-pump. Cultivation, dewatering, thermochemical bio-oil recovery, bio-oil stabilization, conversion to renewable diesel, and transport to the pump.	Harvesting by membrane filtration and centrifugation, followed by thermochemical conversion (hydrothermal liquefaction vs. pyrolysis)	Maize, soybean	Net energy ratio, greenhouse gas emissions.	Hydrothermal liquefaction leads to carbon savings in contrast to pyrolysis. Carbon savings are higher in comparison to maize bioethanol.	Biomass productivities at 6.5 g m^{-2} day^{-1} in Arizona conditions.	(Bennion et al. 2015)
Several species	OP	Upstream resources, cultivation, conversion into biodiesel followed by anaerobic digestion.	Normalization of studies based on cultivation in open ponds, conversion into biodiesel and use of anaerobic digestion.	Maize, soybean	Greenhouse gas emissions	Energy consumption and greenhouse gas emissions would be similar to those obtained for terrestrial alternatives.	Meta-analysis based on six life-cycle assessments for microalgal biofuel production. Functional unit set as 1,000 L biodiesel.	(Liu et al. 2012)
Several species	OP	Several system boundaries based on reviewed studies.	Several technologies based on the reviewed studies.	Rapeseed	Greenhouse gas emissions. Overview for water use, land use, nutrient and fertilizer use, carbon fertilization, fossil fuel inputs, eutrophication, genetically modified algae, algal toxicity.	Decreases in CO_2 for raceway ponds compared to photobioreactors, reaching similar values to those obtained for rapeseed. Major energy inputs are associated with pumping and mixing during cultivation and to the provision of heat for algae drying.	Review of seven life-cycle assessments.	(Slade and Bauen 2013)
Several species	OP, PB	Several system boundaries based on reviewed studies.	Several biomass processing methods including solvent extraction, hydrothermal liquefaction, secretion, pyrolysis, supercritical water, in-situ transesterification.	N.S.	Global warming potential.	Global warming potential varies between production technologies and system boundaries. Thermochemical conversion and anaerobic digestion seem promising alternatives that reduce energy inputs.	Review that includes information about global warming potential for a set of microalgal production technologies.	(Quinn and Davis 2015)

Tetraselmis chui	PB	Cradle-to-grave, including cultivation, harvesting, processing, and products (utilization and consumption).	Harvesting through primary to tertiary dewatering and spray drying, followed by slow pyrolysis, oil extraction by solvent and production of biogas, bio-oil, biodiesel, and biochar.	Rapeseed, soybean	Global warming, abiotic resource depletion (excluding water), land transformation and use, water resource depletion, eutrophication, acidification, eco-toxicity, human toxicity, photochemical smog, ozone depletion, ionizing radiation, respiratory effects.	Lower global warming and land use in comparison to first generation biofuels. Higher eutrophication, water use, ecotoxicity, acidification, photochemical smog and respiratory effects in comparison to first generation biofuels. Improvements are expected if using hydrothermal liquefaction.	The system was modeled in Queensland conditions, Australia. Includes co-product allocation, CO_2 addition from power plant station (13%), water use for evaporative cooling and water recycling. Functional units defined as 1 MJ of pyrolysis biogas combusted for electricity and 1 MJ of pyrolysis bio-oil combusted for electricity or extracted lipid refined for transport fuel.	(Grierson et al. 2013)

3.4 Pesticide and fertilizer pollution

Pesticides and fertilizers can impact vertebrate biodiversity in biofuel crops and non-target areas, negatively affecting native ecosystems. Pesticides can, directly and indirectly, lead to the collapse of vertebrate populations as a result of several mechanisms, including direct poisoning, reduced amounts of prey, increases in occurrence of diseases (Hayes et al. 2006, Parsons et al. 2010, Köhler and Triebskorn 2013, Gibbons et al. 2015), and decreases in fruit productivities when pollinator biodiversity is negatively affected (Potts et al. 2010).

Overuse of fertilizers can pollute soils with heavy metals that bioaccumulate in vertebrates (Atafar et al. 2010) and indirectly alter biodiversity through increases in greenhouse gas emissions (Snyder et al. 2009). Eutrophication of aquatic systems as a consequence of runoff can lead to oxygen depletion and bioaccumulation of toxins produced by toxic algae blooms (Anderson et al. 2002) and occurrence of diseases (e.g., nitrate accumulation in vertebrates) (Guillette and Edwards 2005). Besides the global warming potential of NO_x, increases in nitrogen compounds in the atmosphere have been suggested to reduce plant diversity and alter ecosystem functioning (Holland et al. 1999, Phoenix et al. 2006).

The release of pollutants depends upon the type of biofuel production system and its associated management practices. For example, soybean cropping in the USA uses lower amounts of fertilizers and pesticides when compared to maize, leading to the release of 1% of the N, 8.3% of the P, and 13% of the pesticides, per net energy gain, used for maize ethanol production (Hill et al. 2006). Unlike first generation biofuels, microalgal cultivation does not require the use of pesticides (Lardon et al. 2009, Rodolfi et al. 2009, Brennan and Owende 2010). When grown in photobioreactors, contamination of cultures by pathogens and algae grazers does not often occur (Mata et al. 2010, Chen et al. 2011). In open ponds, methods other than pesticide addition help to decrease the incidence of undesired organisms, such as increases in pH and free ammonia concentrations (Schlüter and Groeneweg 1981, Park et al. 2011, Usher et al. 2014, Schenk 2016).

Microalgal systems make use of fertilizers mainly in the forms of nitrates, ammonium, and phosphate (Slade and Bauen 2013). It has been estimated that the production of 1 Kg of biodiesel from *C. vulgaris* grown in open raceway ponds under California conditions, needs 0.33, 0.71, 0.58, 0.27, and 0.15 Kg of nitrogen, phosphorous, potassium, magnesium, and sulfur respectively (Yang et al. 2011).

At Pinjarra Hills (Brisbane, Australia) the production of 1 Kg of biodiesel from *Scenedesmus dimorphus* requires 0.04 Kg of mono-ammonium phosphate, 0.02 Kg of magnesium sulfate, 0.2 Kg of ammonium sulfate, plus 0.004 Kg of micronutrients (Schenk 2016). However, microalgal systems have lower eutrophication potential than first generation biofuels (Lardon et al. 2009, Clarens et al. 2010, Collet et al. 2011, Hou et al. 2011), primarily because runoff can be controlled in contrast to terrestrial crops (Clarens et al. 2010). In fact, if cultivation wastewater is recycled, fertilizers would not reach aquatic systems, eliminating gray water footprints (Gerbens-Leenes et al. 2014), and reducing nutrient requirements (Yang et al. 2011, Zaimes and Khanna 2013). For instance Yang et al. (2011) estimate that water recycling in open ponds using *C. vulgaris* could reduce fertilizers use by around 55%; and if using seawater or wastewater the use of nitrogen would decrease by 94%. Using sea/wastewater for algal culture can reduce nitrogen usage by 94% and eliminate the need for potassium, magnesium, and sulfur. However, if wastewater reaches aquatic systems negative impacts on biodiversity are expected due to eutrophication (Slade and Bauen 2013, Gerbens-Leenes et al. 2014, Usher et al. 2014, Zhu et al. 2015).

3.5 Water depletion

Water depletion can affect biodiversity associated with water systems, because of direct withdrawals and changes in water quality, including increases in salinity and concentrations of minerals (Matson et al. 1997). The water footprint (WF) can be divided into green WF (volume of rainwater consumed), blue WF (volume of surface and groundwater consumed) and gray WF (volume of polluted water) (Mekonnen and Hoekstra 2011). Microalgal systems have a green and blue WF as a result of evaporative losses in raceway open ponds, evaporative cooling in photobioreactors and evaporation from dry biodiesel conversion routes, while if wastewater is recycled or treated the gray WF should be zero (Gerbens-Leenes et al. 2014). As a consequence, for open ponds in California, the water footprint is expected to be reduced by around 84% if water is recycled, and by around 90% if seawater or wastewater are used (Yang et al. 2011).

Green and blue WFs using wet conversion routes and recycling water are between 2.7 and 32.6 kL per GJ of produced green diesel (Gerbens-Leenes et al. 2014) (Table S12 in Supplementary Information). These values are lower than those obtained for terrestrial biofuel crops such as soybean, sugarcane, maize, rapeseed and sugar beet (Fig. 4). The variation in water requirements is a function of lipid productivity, local weather conditions, and the architecture of the microalgal production system (photobioreactors or open ponds), being highest when using open ponds in places with high evaporation rates (Zaimes and Khanna 2013) and low lipid productivities (Gerbens-Leenes et al. 2014). Other factors that affect water consumption are the medium preference of microalgal strains (fresh, brackish or saline water) and the conversion technologies for biodiesel production (thermal drying and pyrolysis in dry conversion route vs. water reuse in wet conversion route), being higher when using freshwater species and when using dry conversion routes (Gerbens-Leenes et al. 2014). However, water use would be higher if it is not recycled. For instance, Clarens et al. (2010) show that open raceway ponds in Virginia, Iowa, and California conditions, would need more water than rapeseed and maize cropped in the same locations, provided that there is not water recycling.

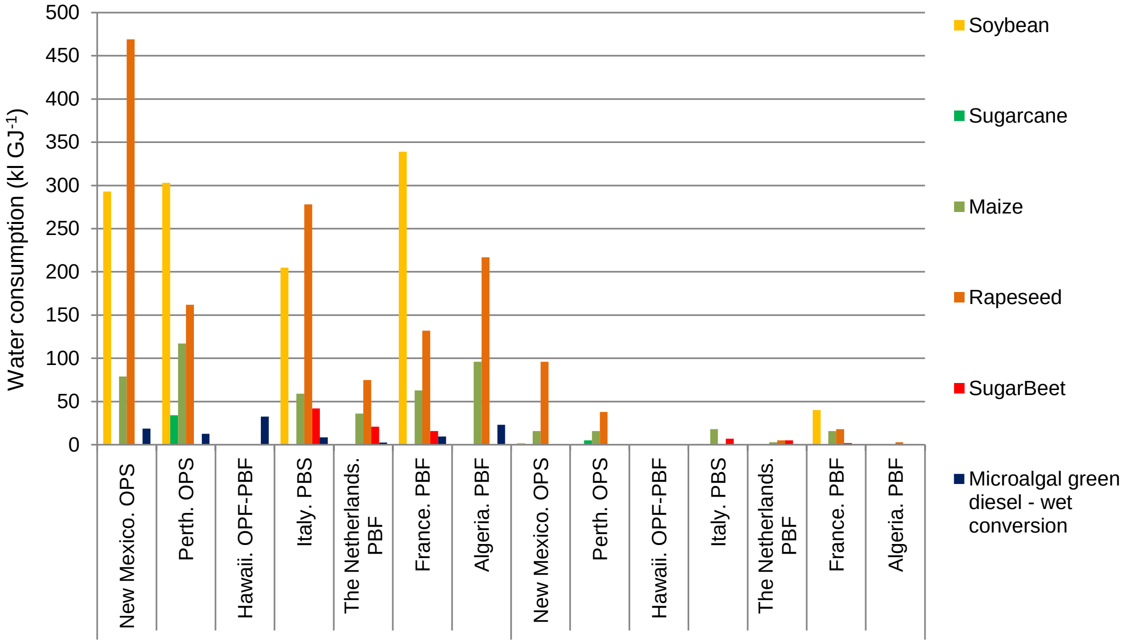

Figure 4. Water consumption per unit of produced energy (GJ) derived from biodiesel (soybean, oil palm, microalgae) and bioethanol (maize, sugarcane).Based on calculations by Gerbens-Leenes et al. (2014) for wet conversion of microalgal biodiesel and assuming water recycling. Available water footprints for first generation biofuels were obtained from Mekonnen and Hoekstra (2011). Microalgal systems in New Mexico and Perth consist of open ponds using salty water (OPS), in Hawaii correspond to a combination of open ponds and photobioreactors using fresh water (OPF-PBF), in Italy consist of photobioreactors using salty water (PBS), and in the Netherlands, France and Algeria consist of photobioreactors using fresh water (PBF).

3.6 Overexploitation of soils

Soils are considered a renewable resource when managed in a sustainable way, by avoiding erosion and maintaining or increasing fertility and soil biodiversity (Doran and Zeiss 2000). Fertile soils increase food security, decrease desertification, help in climate change mitigation and increase biodiversity (Pimentel et al. 1995, Pimentel and Kounang 1998, Lal 2009). Biofuel production systems may negatively affect in-situ soil productivity when using management practices that increase soil erosion and affect physical, chemical and biological properties in soils (e.g., indiscriminate tillage) (Kim and Dale 2005, Anderson-Teixeira et al. 2009). Additionally, soil erosion can negatively affect aquatic biodiversity due to eutrophication, sedimentation and the alteration of physical and chemical properties in aquatic systems (Pimentel and Kounang 1998).

Soils are not used directly for microalgal production systems. However, construction of open ponds could increase soil erosion, soil compaction and alter soil properties including texture and fertility (Zhu and Ketola 2012, Zhu 2015), if soil conservation practices are not implemented. The construction of elevated ponds (e.g., using bricks) could decrease soil removal (which could be around 225,000 and 450,000 tonnes ha^{-1}, assuming pond depths between 15 and 30 cm and soil bulk densities at 1.5 g cm^{-3}), although at higher economic costs. After ponds are constructed, soil erosion is expected to be lower than in agricultural production systems, which have reported erosion rates between 0.5 and 400 tonnes ha^{-1} year^{-1} (Pimentel et al. 1995, Pimentel 2006).

3.7 Increases in invasive species and genetic pollution

Invasive species are a major threat to biodiversity (Wilcove et al. 1998, Crooks 2002). Biofuel crops can increase the occurrence of invasive species within and outside plantations, creating favorable environmental conditions for the arrival and persistence of invasive organisms (Richardson and Rejmánek 2011). Furthermore, some species may become invasive as a result of their increased propagule production, dispersal and/or persistence abilities (Raghu et al. 2006, Chimera et al. 2010). Crops like sugarcane, soybean, sugar beet and maize are not considered invasive, while others have traits that increase their invasiveness potential (e.g., rapeseed produces large seed quantities that can be dispersed by a wide arrange of agents, and can hybridize with wild native varieties) (Chimera et al. 2010, Davis et al. 2010) (Table 2). As a consequence, it has been estimated that terrestrial plants suitable for biofuel production have two to four times higher potential than other crops to become naturalized or become invasive (Buddenhagen et al. 2009, Chimera et al. 2010).

In relation to microalgal production systems, the potential invasion of water systems could happen if leakage of growth medium, which may include genetically engineered species, occurs (Fargione et al. 2009, Zhu and Ketola 2012, Slade and Bauen 2013). This is because the same traits that allow them to grow in a wide range of environmental conditions predispose them to invasiveness potential (Phalan 2009). If toxic species are released (e.g., *Anabaena circinalis, Oscillatoria agardhii, Cylindrospermopsis raciborskii*) unexpected changes in ecosystem function could occur under favorable environmental conditions (e.g., expansion of toxic algae blooms in eutrophic aquatic systems) (Chimera et al. 2010, Ditomaso et al. 2010). However, if native or local microalgal strains are used for biofuel production, or if water is recycled, invasion potential is expected to decrease.

Table 2. Comparison of widely used first generation biofuel crops in relation to their potential for genetic pollution and invasiveness.

Biofuel crop	Center of origin	Dispersal units	Non-human effective dispersal vectors	Reported genetic pollution	Reported invasiveness
Oil palm (*Elaeis guineensis*)	Tropical Africa (Corley and Tinker 2015)	Seeds	Animals	No	Yes (Meyer 2000, Gordon et al. 2011)
Maize (*Zea mays*)	Americas	Seeds	N.A.	Yes (Viljoen and Chetty 2011, Chaparro-Giraldo and López-Pazos 2015)	No
Rapeseed (Brassica napus)	Mediterranean region (Rakow 2004)	Seeds	Autochory, wind, water, animals (Australian Government 2008)	Yes (Rieger et al. 2002, Knispel and McLachlan 2010)	Yes (Pessel et al. 2001, Kawata et al. 2009)
Sugarcane (*Saccharum* sp.)	Tropical region (Moore et al. 2013)	Cuts, seeds (low viability of seeds)	N.A.	No	No
Soybeans (*Glycine max*)	China	Seeds	Autochory (Yoshimura et al. 2011)	Yes (Kuroda et al. 2006, Mallory-Smith and Zapiola 2008)	No

3.8 Emissions of air pollutants and changes in factors that affect regional climate

In addition to greenhouse gasses (section 3.3), the production and use of biofuels generate toxic substances that are released into the air, and that can negatively impact ecosystem functions and biodiversity. These pollutants include nitrogen oxides (NO_x), ammonia (NH_3), carbon monoxide (CO), volatile organic compounds (VOC), particulate matter (PM), oxides of sulfur (SO_x) (Zhang et al. 2016), methyl bromide (CH_3Br) (Ristaino and Thomas 1997) and nitrous oxide (N_2O) (Ravishankara et al. 2009). They are produced during cropping (e.g., as a result of fuel combustion by the operation of machinery, and as a consequence of chemical applications and soil disturbance), biofuel production and combustion (Zhang et al. 2016), as well as during the construction of facilities and the extraction and shipping of resources (Collet et al. 2011). They lead to increases in acidification (i.e., acid rain), ozone layer depletion, and photochemical oxidation, among other environmental impacts (Heijungs et al. 1992). Their effects include changes in the structure and function of both terrestrial and aquatic ecosystems, which include alterations in species composition (Barker and Tingey 1992, Sala et al. 2000, Lovett et al. 2009).

The release of pollutants differs among biofuel production systems. For instance, taking into account total life-cycle emissions, it has been shown that soybean biodiesel produced in the USA releases less air pollutants when compared to corn ethanol per net energy gain (Hill et al. 2006), while corn grain ethanol blended with gasoline (E-85) increases the amount of emitted pollutants (CO, VOC, PM10, NOx, SOx) in comparison to gasoline per unit of energy released upon combustion (Wang et al. 2005). After accounting for cultivation and harvesting, it is estimated that in the USA corn grain ethanol would emit more pollutants per produced gallon than ethanol from switchgrass, corn stover, wheat straw and forest residues (Zhang et al. 2016).

Compared to first generation biofuels, emission of air pollutants can be lower for microalgal systems (Collet et al. 2011, Hou et al. 2011). Collet et al. (2011) estimated that biodiesel produced from *C. vulgaris* grown in open raceway ponds in Mediterranean conditions coupled with anaerobic digestion and assuming low-energy cultivation systems, led to lower potential acidification, ozone layer depletion and photochemical oxidation per MJ of combusted fuel than first generation biofuels after accounting for extraction and shipping of resources, cultivation, biofuel production, and construction and dismantling of facilities. Using the same species and open raceway ponds in Mediterranean conditions, Lardon et al. (2009) found lower acidification potential in comparison to rapeseed, but higher ozone layer depletion and photochemical oxidation when compared to first generation biofuels. However, they did not account for nutrient recycling (e.g., using anaerobic digestion), which would lead to lower energetic burdens and decrease air pollutants.

Air pollution may also impact biodiversity via changes in atmospheric temperature and weather patterns: the release of substances that increase tropospheric ozone (CO, NO_x, VOC, CH_4) exacerbates global warming potential, while the release of aerosol particles (including sulfate, organic carbon, black carbon, biomass burning, nitrate, and mineral dust aerosols) increase albedo and thus exert an atmospheric cooling effect (Forster et al. 2007). Furthermore, it has been shown that aerosols affect not only cloud albedo but also the size and number of droplets in clouds, which can alter precipitation regimes worldwide depending on meteorological conditions (Forster et al. 2007, Rosenfeld et al. 2008, Li et al. 2011). Changes in surface albedo (that result from land-use change), coupled with increases in tropospheric ozone and aerosols, can alter atmospheric temperature and precipitation patterns, with potential impacts on ecosystems. While deforestation for biofuel production would decrease regional humidity and increase atmospheric temperature, evaporation from microalgal ponds could have the opposite effect (Usher et al. 2014), with potential increases in regional precipitation and additional cooling effects as water evaporates (Forster et al. 2007).

3.9 Considerations for the adoption of sustainable biofuel production systems

Transforming biodiverse landscapes into biofuel cropping systems is a detrimental practice for the short and long-term conservation of biodiversity. Biofuel production should only be promoted where few direct and indirect impacts on biodiverse systems are expected; implying that crops with low biofuel yields or crops that compete with available lands for agriculture or for the conservation of biodiversity should be avoided. Currently, biofuel is primarily produced from suboptimal crops that do not have the highest biofuel yields (Figs. S1 to S5, Tables S7 to S11 in Supplementary Information) and that compete with agricultural lands or highly biodiverse landscapes. Thus, biofuel production systems, management practices and production technologies that have lower environmental footprints should be encouraged. This means that only systems with low potential to cause direct and indirect land-use change of agricultural lands and biodiverse regions and that offer higher carbon savings should be deployed, and also those systems with high freshwater consumption, high potential for pollution, soil degradation, and high invasiveness should be avoided.

4. CONCLUSIONS

The main pressures negatively impacting biodiversity due to biofuel production are direct and indirect land-use changes, particularly when ecosystems with high biodiversity values (e.g., tropical and subtropical forests and native grasslands) are transformed into biofuel crops. Several other pressures that negatively impact biodiversity include greenhouse gas emissions, pesticide and fertilizer pollution, water depletion, overexploitation of soils, invasive species and genetic pollution, emissions of air pollutants and changes in factors that affect regional climate (e.g., alterations in albedo and evapotranspiration patterns), which directly or indirectly impact biodiversity.

Biofuel production systems and their associated management practices influence the magnitude of the impacts on biodiversity. Systems with higher productivity per unit area are expected to lead to less direct and indirect land-use changes, especially if their cultivation does not occupy fertile agricultural lands and does not compete with areas of high biodiversity value. Higher greenhouse gas savings would be achieved both when transforming low carbon systems (e.g., eroded lands) into biofuel crops and when using biofuel systems with lower energy intensive processes. Pollution would be reduced through the adoption of systems with lower fertilizer and pesticide inputs, combined with less energy intensive processes that are currently powered by fossil fuels. Furthermore, biofuels and their associated management practices can be designed to achieve better water efficiencies, less soil degradation (e.g., low soil erosion), and reduced invasive potential.

We estimated that microalgal production systems would need substantially less cultivation area compared to first generation biofuels per unit of produced energy, making them the most feasible option in terms of reduced land needs, especially within tropical and subtropical regions of the world where they achieve higher productivities. Limiting their cultivation to degraded lands would additionally lead to lower biodiversity impacts in comparison to any first generation biofuel production system. Open ponds are the preferred system for increasing carbon savings, because of their lower energy-intensive production processes compared to photobioreactors. Increased carbon savings in microalgal systems can be achieved through the optimization of productivities per unit area, their colocation with industrial CO_2 sources or wastewater systems, and the implementation of technologies that allow nutrient recycling and energy production (e.g., utilizing anaerobic digestion and re-using water). Increases in energy efficiencies (e.g., using wet conversion routes for biodiesel production and replacing external fossil energy sources) are expected to reduce greenhouse gas emissions. Increased energy efficiencies and nutrient recycling are also expected to decrease emissions of air pollutants (NO_x, NH_3, CO, VOC, PM, SO_x, N_2O). Moreover, water recycling is essential to reduce gray water footprints, avoid pollution derived from potential growth media releases and decrease the chances of spreading invasive and potentially harmful microalgal strains. Finally, we call for a better inclusion of biodiversity in future studies on environmental impacts of biofuel production systems as it is currently underrepresented, particularly in life-cycle assessments (Guinée et al. 2010, Cherubini and Strømman 2011, Wiloso et al. 2012).

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Chapter 1: Supplementary Information

1. Studies relating to biofuels and biodiversity

Tables S1 and S2 summarize the information associated with selected studies relating biofuels and biodiversity in tropical and subtropical regions of the world, using the Science Citation Index Expanded (SCI-EXPANDED) and the Emerging Sources Citation Index (ESCI) in Web of Science, based on the following combination of keywords: (biofuel OR bioenergy) AND (biodiversity OR wildlife), (biofuel OR bioenergy) AND (fish* OR bird* OR avian OR mammal* OR reptil* OR amphibian*).

Table S1. Specific studies that relate to biofuels and biodiversity.

Biofuel crop	Group of terrestrial vertebrates	Location	Timeframe	Main methods	Identified pressures	Initial land- use	Main impact indicators	Main impacts	Reference
First (maize, soybean) and second generation biofuels	Birds	Americas (Upper Midwest states - USA)	N.S.	Simulations. Modeling of potential richness of birds under future expansion of bioenergy crops	Land-use change	Agricultural lands, marginal lands	Richness of species including threatened species	Decreases in richness of species if maize or soybeans replace marginal lands. Increases in richness if agricultural lands are replaced by second generation biofuel crops	(Meehan et al. 2010)
First (maize, soybean) and second generation biofuels	Birds, mammals, amphibians	Africa	2050	Spatial analyses. Estimation of carbon emissions and biodiversity losses under potential future increased crop cultivation	Land-use change, greenhouse gas emissions	Wet savannas	Habitat loss	Widespread habitat losses and high greenhouse gas emissions if wet savannas are transformed into crops	(Searchinger et al. 2015)
First (maize, sugarcane) and second generation biofuels (corn stover)	N.S.	Americas (Brazil, USA)	2020, 2030	Assessment of land demands between feedstocks for fulfilling energy demands according to IEA biofuel use scenarios	Land-use change, greenhouse gas emissions	N.S.	Habitat loss	Expected habitat losses as a result of increases in land demands for biofuel production	(Leal et al. 2013)
First (sugar beet, rapeseed) and second generation biofuels (bermudagrass)	Birds, mammals, amphibians, reptiles	Americas (California - USA)	2050	Spatial analyses. Assessment of potential impacts of crops on wildlife based on current and potential biofuel crops, suitable land and species suitability models	Land-use change, land-use intensification, water depletion	Agricultural lands	Habitat loss	Higher habitat losses for canola crops	(Stoms et al. 2012)
First and second generation biofuels	N.S.	Asia (India)	2020	Assessment of environmental impacts of increased biofuel production	Land-use change (direct, indirect), land-use intensification, greenhouse gas emissions, water depletion, pesticide and fertilizer pollution, invasive species	Wastelands, degraded grasslands	Habitat loss	Expected less habitat loss if using wastelands and degraded habitats for biofuel production	(Ravindranath et al. 2011)
First and second generation biofuels	Birds, mammals, amphibians, reptiles	Global	N.A.	Review of the impacts of biofuel production on biodiversity	Land-use change (direct, indirect), land-use intensification, greenhouse gas emission, invasive potential of crops, pesticide and fertilizer pollution	Agricultural lands, marginal and degraded lands, native ecosystems	Habitat loss	Habitat and biodiversity losses are higher for first generation biofuels, when native ecosystems are transformed into biofuel crops in tropical regions. Biodiversity impacts of perennial crops can be positive, but still are a matter of debate.	(Immerzeel et al. 2014)
First and second generation biofuels	N.S.	Europe	2000-2030	Simulations. Determination of potential areas of land-use change under three different biofuel development scenarios	Land-use change, land-use intensification, pesticide and fertilizer pollution	Croplands, pastures	Habitat loss	Higher habitat loss if croplands and surplus pasture lands are transformed into biofuel crops	(Fischer et al. 2010)
First and second generation biofuels	N.S.	Global	2020	Simulations. Determination of potential direct and indirect land-use changes as a result of the European Union biofuel targets	Land-use change (direct, indirect), land-use intensification	Cropland, grassland, short rotation tree plantation, managed forests, natural forests and other natural lands.	Habitat loss	Habitat loss in high biodiversity areas	(Frank et al. 2013)
First and second generation biofuels	N.S.	Global	2000-2050	Simulations. Simulation of potential land-use changes caused by feedstock production under five development scenarios	Land-use change, land-use intensification, increases in greenhouse gas emissions, water depletion	Agricultural lands, native ecosystems	Habitat loss, habitat perturbation	Habitat loss, lower for scenarios that target not further deforestation. Increases in habitat perturbation as a result of increased forest management practices	(Kraxner et al. 2013)
First and second generation biofuels	N.S.	Global	2050	Simulations. Use of a biophysical biomass-balance model for predicting bioenergy crop potentials	Land-use change, land-use intensification, pesticide and fertilizer pollution	Croplands, forests, unused areas, others	Habitat loss	Higher habitat loss if biofuel cropping increases. Intensification also leads to habitat loss.	(Erb et al. 2012)
First and second generation biofuels	N.S.	Africa (South Africa)	21st century	Spatial analyses about potential distribution and land availability for different biofuel crops	Land-use change, land-use intensification	Native ecosystems	Habitat loss	Habitat loss if areas with high ecological value are transformed into biofuel crops	(Blanchard et al. 2015)
First and second generation biofuels	N.S.	Europe	2005	Spatial analyses. Estimation of wetland distribution and suitable wetland restoration sites under different policies	Land-use change (direct-indirect), land-use intensification, greenhouse gas emissions associated to wetland conversion into agricultural lands	Wetlands, agricultural lands, forests, nature reserves	Habitat loss	Habitat can be lost within Europe and outside Europe as a result of leakage effects	(Schleupner and Schneider 2010)
First and second generation biofuels	Birds, mammals, amphibians, reptiles	Europe (EU-27)	2000-2030	Spatial analyses. Land-use change simulations for three biofuel policy options coupled with species-specific	Land-use change (direct, indirect)	Several land covers including forests, semi-natural vegetation and agricultural lands	Habitat loss, species composition	Loss of habitat for most species under increased biofuel targets. Higher habitat losses when using non-woody biofuel crops. Changes in species composition.	(Eggers et al. 2009)

				information on habitat suitability					
First and second generation biofuels	N.S.	Global	1990-2035	Spatial analyses. Simulations of biofuel expansion under different development scenarios	Land-use change (direct-indirect), land-use intensification, greenhouse gas emissions	Agricultural lands, native ecosystems including forests and grasslands	Habitat loss	Habitat loss as biofuels crops expand	(Prieler et al. 2013)
First generation biofuels	N.S.	Global (12 developed and developing countries)	2000-2013	Assessment of the relationships between biofuel production, consumption and environmental indicators	Land-use change (direct, indirect), agriculture intensification, greenhouse gas emissions	Arable lands, forests	Habitat loss	Inferred habitat losses within agricultural areas	(Ozturk 2016)
First generation biofuels	Birds	Americas (Argentina)	2003-2006	Field surveys for richness and abundance of species comparing native ecosystems and agricultural lands (including crops, pastures and ploughed areas)	Land-use change, land-use intensification	Native woodlands, agricultural lands	Richness and abundance of native species, species composition	Decrease of species richness and changes in species composition. Several raptors are positively related to agricultural lands.	(Schrag et al. 2009)
First generation biofuels	Birds, mammals	Americas (USA)	N.A.	Review and meta-analysis evaluating diversity values of biofuel crops in relation to s that they have replaced	Land-use change (direct, indirect), land-use intensification, pesticide and fertilizer pollution, increases in greenhouse gas emissions (increased global warming)	Natural habitats (e.g. coniferous forests), low-intensity land uses (e.g. pastures), row-crops	Richness and abundance of native species, richness and abundance of threatened species	Decrease in richness and abundance of native species, higher in row crops than in pine or poplar plantations. Decreases for threatened bird species, especially in maize crops. There are expected increases in richness and abundance of birds when row-crops are converted into biofuel perennial crops.	(Fletcher et al. 2011)
First generation biofuels	Birds	Americas (USA)	N.A.	Review of studies and datasets on richness and abundance of grassland birds comparing biofuel crops	Land-use change	N.S.	Richness and abundance of native species, richness and abundance of threatened species	Lower richness and abundance of native and threatened species in maize crops when compared to perennial plants. Potential of habitat provision for grassland birds including threatened species using native perennial plants (switchgrass, mixed grass–forb prairies)	(Robertson et al. 2012)
First generation biofuels	N.S.	Global	2000-2030	Spatial analyses. Estimation of potential land-use changes as a result of European agricultural and biofuel policies	Land-use change (direct-indirect), land-use intensification, greenhouse gas emissions	Agricultural lands, native ecosystems including grasslands and forests	Habitat loss	Habitat loss increases especially in Sub-Saharan Africa, Latin America and Asia	(Prins et al. 2011)
First generation biofuels	N.S.	Europe (EU-27)	2000-2030	Spatial analyses. Modelling of potential land use-changes using four scenarios for allocation of biofuel crops coupled with environmental and economic models, exploring two biofuel policies	Land-use change (direct, indirect), land-use intensification	High nature value farmlands, forests, semi natural vegetation	Habitat loss	Loss of habitat as a result of replacement of natural habitats and extensive agricultural lands.	(Hellmann and Verburg 2010)
First generation biofuels (including soybean)	Birds	Americas (Argentina)	1993-2008	Field surveys. Measurements for presence of species in agricultural systems and comparison to historical observations	Land-use change, land-use intensification	Native grasslands	Presence of native species	Decrease in presence of native wetland and grassland specialists. Habitat generalists and woodland specialist did not show any decrease.	(Codesido et al. 2011)
First generation biofuels (including soybean, maize, oil palm, sugarcane)	N.S.	Tropical region	1999-2030	Spatial analyses. Overlapping of future potential agriculture expansion areas and conservation priorities	Land-use change, greenhouse gas emissions	Agricultural lands, native ecosystems	Habitat loss	Habitat loss as a result of overlapping with high biodiverse areas and suitable areas for cropland expansion	(Phalan et al. 2013)
First generation biofuels (maize, soybean, sugarcane, rapeseed) sunflower, and oil palm)	N.S.	Gobal	2030	Spatial analyses. Projection of future development threat for biofuels	Land-use change	Natural lands	Habitat loss	Increases in habitat loss	(Oakleaf et al. 2015)
First generation biofuels (maize, sugar beet)	N.S.	Americas (California - USA)	2010	Simulations. Determination of potential land-use changes for different ethanol production targets	Land-use change, land-use intensification	Croplands, native ecosystems	Habitat loss	Habitat loss, higher if corn is used when compared to sugar beet	(Geyer et al. 2010)
First generation biofuels (oil palm)	Birds	Asia (Malaysia, Indonesia)	1990-2005	Assessment of land use changes using FAO national statics on crop and forest area and evaluation of its impacts on bird diversity	Land-use change, land-use intensification	Primary or secondary (logged) forests, croplands (rubber)	Habitat loss, richness of native species	Decrease of bird richness, higher when converting native forests than rubber plantations.	(Koh and Wilcove 2008)

First generation biofuels (oil palm)	Mammals (focus on Leopard cat and murids)	Asia (Malaysia)	1993-1995	Field surveys for habitat use of leopard cat, distribution and abundance of their preys in different land covers	Land-use change	Selectively logged dipterocarp forest, secondary forest	Habitat selection of leopard cat, richness and abundance of murids	Increase of occurrence of leopard cat in oil palm plantations. Murid relative abundance decreased in oil palm plantations.	(Rajaratnam et al. 2007)
First generation biofuels (oil palm)	Birds	Asia (Malaysia)	2009	Field surveys. Comparison between different management systems	Land-use change, land-use intensification	Peat swamp forest	Richness and abundance of native species, richness and abundance of threatened species, species composition	Decrease in richness and abundance of native and threatened species in oil palm plantations. Species composition between large and small plantations is similar, but large plantations have lower species richness.	(Azhar et al. 2013)
First generation biofuels (oil palm)	Birds, mammals, amphibians, reptiles	Tropical region	N.A.	Review and meta-analysis of studies relating biodiversity and oil palm plantations	Land-use change (direct, indirect)	Primary forest, logged-over forest, secondary forest scrubland, grassland, cropland	Species richness and abundance, species composition	Species richness decreases in oil palm plantations, species assemblages changes and forest specialists decrease	(Savilaakso et al. 2014)
First generation biofuels (oil palm)	Birds, mammals, reptiles	Tropical region (Indonesia, Dominican Republic, Thailand, Malaysia)	N.A.	Review and meta-analysis on studies that compare diversity between forests and oil palm plantations	Land-use change, land-use intensification, increases in greenhouse gasses emissions (result of land-use change), water depletion (hydrological changes), emission of air pollutants, pesticide and fertilizer pollution.	Primary forests	Richness and abundance of native species, richness and abundance of threatened species, species composition	Decrease in richness and abundance of native forest species with high ecological requirements including threatened species, increases in richness of generalist species	(Danielsen et al. 2009)
First generation biofuels (oil palm)	Birds, mammals, amphibians, reptiles	Americas (Focus on Colombia)	N.A.	Review of environmental impacts of oil palm plantations	Land-use change, land-use intensification	Agricultural lands, native ecosystems (including forests and savannas)	Habitat losses, diversity of native and threatened species	Current and expected habitat losses as a result of oil palm expansion. Presence of generalist species within oil palm plantations. Potential lower biodiversity losses or even gains if pastures are transformed into oil palm plantations while conserving surrounding forests.	(Vargas et al. 2015)
First generation biofuels (oil palm)	Birds, mammals, reptiles	Asia (Focus on Malaysia and Indonesia)	N.A.	Review. Comparison of biodiversity in native forests, oil palm plantations and alternative uses	Land-use change, land-use intensification, pesticide and fertilizer pollution, increases in greenhouse gas emissions (result of land-use change), increases in invasive species	Native forests, *Imperata* grasslands, crops (rubber, cocoa, coffee, *Acacia mangium*)	Habitat loss, richness and abundance of species, richness and abundance of threatened species	Decrease in species richness and abundance of native species with high ecological requirements, increase in richness and abundance of generalist species. Increase in forest species for *Imperata* grasslands.	(Fitzherbert et al. 2008)
First generation biofuels (oil palm)	Mammals (Great apes)	Africa (Tropical Africa)	N.A.	Review. Determination of conflicts between great apes and potential oil palm plantations	Land-use change, land-use intensification	Tropical forests	Habitat loss	Habitat loss for great apes if suitable areas for oil palm plantations are transformed, increase of conflicts between apes and farmers	(Wich et al. 2014)
First generation biofuels (oil palm)	N.S.	Asia (Indonesia)	2020	Simulations. Simulation of potential land-use changes under different development scenarios (business-as-usual, food production, forest preservation, carbon conservation, hybrid approach)	Land-use change (direct, indirect), land-use intensification	Agricultural lands, tropical forest	Habitat loss, biodiversity loss	Habitat and biodiversity losses in most scenarios, except if degraded and agricultural lands are transformed into oil palm plantations	(Koh and Ghazoul 2010)
First generation biofuels (oil palm)	N.S.	Americas (Peru)	2000-2010	Spatial analyses. Calculation of land-use change based on satellite images	Land-use change, land-use intensification	Native lowland forests	Habitat loss	Habitat loss for native species, greater for high-yield plantations	(Gutierrez-Velez et al. 2011)
First generation biofuels (oil palm)	Birds	Australasia (Papua New Guinea)	1989-2000	Spatial analyses. Estimation of deforestation using satellite images and assessing of conservation status of birds based on the IUCN criteria	Land-use change	Native forests	Habitat loss, number of threatened species	Loss of habitat for native and endemic species, Increase in number of threatened species as a result of habitat loss	(Buchanan et al. 2008)
First generation biofuels (oil palm)	Birds	Asia (Southeast Asia)	2000-2010	Spatial analyses. Estimation of replacement of native forests into oil palm plantations based on satellite images and model of biodiversity impacts	Land-use change, greenhouse gas emissions as a result of land-use change	Native forests including peat swamp forests	Habitat loss, loss of native species	Habitat loss for native species and local extinction of native species	(Koh et al. 2011)
First generation biofuels (oil palm, soybean)	N.S.	Tropical region (Indonesia, Malaysia, Brazil, Argentina)	Mid 1990-early 2000	Assessment of socioeconomic and biodiversity impacts of agriculture development on biodiversity between the selected periods of time, taking into account production, socioeconomic and biodiversity indicators	Land-use change (direct, indirect), land-use intensification	Natural ecosystems, extensive land use and intensive croplands	Indicators based on the Natural Capital Index (NCI)	Decrease of biodiversity as a result of agriculture expansion and intensification in most production areas. Biodiversity losses were lower in areas already transformed for agricultural purposes.	(Kessler et al. 2007)
First generation biofuels (oil palm, sugarcane)	N.S.	Tropical region	2050, 2100	Spatial analyses. Modelling of land competition for biofuel crop production vs.	Land-use change (direct, indirect)	Tropical forests	Habitat loss	Increases in habitat loss were biofuel production is more profitable than conservation for carbon payments	(Persson 2012)

				conservation for carbon payments					
First generation biofuels (soybean)	N.S.	Americas (Bolivia, Paraguay, Brazil)	1990s-2000s	Assessment. Modelling of relationships between deforestation and changes in exchange rates between US dollar and local currencies	Land-use change(direct-indirect), land-use intensification	Agricultural lands, native ecosystems	Habitat loss	Habitat loss as a result of currency fluctuations, displacement of cattle farms to the Amazon region	(Richards et al. 2012)
First generation biofuels (sugarcane, soybean)	N.S.	Americas (Brazil)	2006	Spatial analyses. Identification of available "residual lands" with low biodiverse value for biofuel production	Land-use change (direct, indirect)	"Residual lands" outside the Amazon region and protected areas, and with low biodiversity value	Habitat loss	Less habitat losses are expected if using "residual lands" outside protected areas and outside the Amazon region for biofuel production	(Lossau et al. 2015)
First generation biofuels (including soybean)	Birds (Raptors)	Americas (Argentina)	2002-2005	Field surveys. Measurement for richness and abundance of raptors along roads.	Land-use change, land-use intensification	Native ecosystems in five biomes: Paraná forest, Espinal, Pampas, Patagonian forest, Monte desert	Diversity, richness and abundance of raptors	Decreases in diversity, richness and abundance of raptors, including endemic and rare species, in transformed areas with fragmented native ecosystems	(Carrete et al. 2009)
N.S.	Birds	Americas (Brazil)	2005	Field surveys, simulations. Measurement of richness and abundance of birds in agricultural matrices. Simulations of potential local bird extinction under different land-use scenarios	Land-use change, land-use intensification	Tropical forest	Richness and abundance, species composition	Habitat loss for forest dependent species, increase in number of generalist species. Additional losses are expected if relictual large trees are removed.	(Mahood et al. 2012)
N.S.	N.S.	Global	2050	Simulations. Prediction of areas needed to satisfy global energy demands	Land-use change, land-use intensification, water depletion, greenhouse gas emissions (soil carbon losses)	Croplands, native ecosystems	Habitat loss	Great habitat losses if biofuels become a major energy source	(Haberl et al. 2013)
N.S.	N.S.	Global	1995-2050	Simulations. Simulation of impacts on mean species abundance under difference scenarios of pressures and policies (climate-change mitigation using bioenergy, increases in plantation forestry, increases in protected areas)	Land-use change, land-use intensification, greenhouse gas emissions, pesticide and fertilizer pollution	Native ecosystems, agricultural lands among others	Mean species abundance (MSA)	Decreases in MSA especially when using extensive biofuel crops for climate change mitigation. Grasslands and savannas are more vulnerable to land conversion.	(Alkemade et al. 2009)
N.S.	N.S.	Americas (Brazil)	N.S.	Spatial analyses. Assessment of the compliance of current agricultural lands with environmental legislation of existing agricultural lands and environmental legislation	Land-use change (direct-indirect)	Agricultural lands, native ecosystems	Habitat loss	Habitat has been lost, and there are mismatches between agricultural areas and environmental legislation. Potential leakage effects if current legislation is followed.	(Sparovek et al. 2010)
N.S.	N.S.	Global	2020	Spatial analyses. Estimation of the economic and environmental impacts of European sustainability requirements (EFA proposal)	Land-use change (direct, indirect), land-use intensification, pollution through fertilizers, increases in greenhouse gas emissions	Agricultural areas, grasslands, native ecosystems, marginal lands	Habitat loss	Habitat loss in European marginal lands as a result of agriculture intensification, habitat loss and intensification outside Europe as croplands expand	(Pelikan et al. 2015)

Table S2. Reviews, overviews and general assessments relating biofuels and biodiversity in tropical and subtropical regions of the world.

Biofuel crop	**Reported group of terrestrial vertebrates**	**Location**	**Main methods**	**Main identified pressures**	**Initial land- use**	**Main impacts**	**Reference**
First (focus on maize), second and third generation biofuels (microalgae)	Birds, mammals, fishes	Americas (USA)	Assessment of the impacts of biofuel production on wildlife	Land-use change, land-use intensification, pesticide and fertilizer pollution, water depletion, invasiveness potential, overexploitation of soils (e.g. reduction in fertility when corn stover is used for biofuel production)	Agricultural lands, abandoned lands, native prairies	Habitat loss for native species, impacts on aquatic diversity as a result of eutrophication and algae blooms	(Fargione et al. 2009)
First (including sugarcane) and second generation biofuels (Jatropha)	Birds	Africa (sub-Saharian)	Review of current environmental impacts of biofuel production and biofuel production prospects	Land-use change, greenhouse gas emissions, pesticide and fertilizer pollution, water depletion	Agricultural lands, native ecosystems	Habitat loss, reported decreases in richness and abundance of birds	(Gasparatos et al. 2015)
First (maize) and second generation biofuels	N.S.	Global	Review of available technologies for the reduction in global warming, air pollution, and energy security	Land-use change (direct, indirect), land-use intensification, greenhouse gas emissions, air pollution, water depletion, pollution by wastes (e.g. sewage effluents)	Agricultural lands, native ecosystems	Habitat loss, higher when native ecosystems are transformed into biofuel crops	(Jacobson 2009)
First (maize, soybean) and second generation biofuels	Birds	Americas (USA)	Overview of alternatives for biofuel production in the USA based on Meehan et al. (2010) simulations on potential increases in bioenergy crop cultivation	Land-use change, greenhouse gas emissions, pollution through fertilizer use	Agricultural lands, marginal lands	Decreases in richness of species when using maize or soybeans. Increases in richness if agricultural lands are replaced by second generation biofuel crops	(Fargione 2010)
First (maize, soybean, sorghum, sugarcane, oil palm) and second generation biofuels	N.S.	Americas	Review of current and potential conflicts between biofuel production and biodiversity	Land-use change, pesticide and fertilizer pollution, invasive species	Agricultural lands, marginal lands, native ecosystems	Habitat loss (initially as forests are converted into pastures and later as a result of intensification), higher for first generation biofuels	(Kline et al. 2015)
First (oil crops for biodiesel) and second generation biofuels	N.S.	Global	Review of the role of degraded lands on biodiversity conservation	Land-use change (direct, indirect), invasive species	Degraded lands	Expected habitat losses if degraded lands are transformed into biofuel crops, especially when significant biodiversity values are still retained	(Plieninger and Gaertner 2011)
First (soybean, oil palm) and second generation biofuels	N.S.	Tropical region	Review of the future impacts of agriculture expansion, including biofuel systems, in biodiversity	Land-use change (direct, indirect), land-use intensification, greenhouse gas emissions, increases in infrastructure (e.g. roadways), water depletion, pesticide and fertilizer pollution	Agricultural lands, native ecosystems	Expected habitat losses and biodiversity declining, biotic homogenization	(Laurance et al. 2014)
First (sugarcane, oil palm) and second generation biofuels (*Jatropha,* castor oil)	N.S.	Africa	Review and assessment of environmental impacts of biofuel production in Africa	Land-use change, land-use intensification, greenhouse gas emissions, water depletion, soil overexploitation, invasive potential, pesticide and fertilizer pollution	Native ecosystems (forests, woodlands, wetlands), agricultural lands, marginal lands	Loss of habitat for native species, decreases in richness of native species, potential increases in habitat availability if marginal lands are converted into perennial crops	(Senelwa et al. 2012)
First (sugarcane, sugar beet, sunflower, canola, soybean) and second generation biofuels	N.S.	Africa (South Africa)	Assessment of impacts of South African biofuel strategy for the sustainable production of biofuels in South Africa	Land-use change (direct, indirect), land-use intensification, invasive species, greenhouse gas emissions, pesticide and fertilizer pollution, overexploitation by soils (e.g. use of crop wastes may impact soil fertility), genetic pollution	Native ecosystems, agricultural lands	Potential habitat loss in non-protected areas, habitat perturbation (e.g. changes in fire regimes, micro-climate, phenology)	(Blanchard et al. 2011)
First and second generation biofuels	Birds	Global	Overview of environmental impacts of biofuel production	Land-use change (direct, indirect), pesticide and fertilizer pollution, greenhouse gas emissions, water depletion, emission of air pollutants (e.g. ozone production)	Native ecosystems, degraded or abandoned agricultural lands	Expected biodiversity losses associated with biofuel expansion. Biodiversity losses can also occur in degraded or abandoned agricultural lands	(Scharlemann 2008)
First and second generation biofuels	Birds, mammals	Global	Review of the environmental impacts of biofuels	Land-use change (direct, indirect), land-use intensification, greenhouse gas emissions, pesticide and fertilizer pollution, emission of air pollutants, water depletion, invasive potential	Native ecosystems, agricultural lands	Loss of habitat for native species, decreases in richness of native species, impacts on aquatic and groundwater dependent ecosystems	(Reijnders 2012)
First and second generation biofuels	Birds, mammals, amphibians, reptiles	Europe	Review of the current and future impacts of biofuel production in biodiversity	Land-use change (direct, indirect), land-use intensification, pesticide and fertilizer pollution, greenhouse gas emissions, overexploitation of soils (e.g. soil organic carbon), water depletion	Agricultural lands, native ecosystems	Habitat loss, decreases in biodiversity especially for first generation biofuels, perennial crops may increase biodiversity of vertebrates	(Gabrielle et al. 2014)
First and second generation biofuels	N.S.	Americas (USA)	Review of the opportunities and risks of biofuel production on USA environment	Land-use change, land-use intensification, greenhouse gas emissions, pesticide and fertilizer pollution, overexploitation of soils (e.g. soil erosion)	Agricultural and marginal lands	Potential habitat losses and perturbation if bioenergy crops and forest harvest biomass increase. Potential environmental benefits (reductions in greenhouse gas emissions and air pollutants including SOx) if perennial plants are intercropped or if annual crops are replaced by perennial crops in marginal or sensitive lands.	(Cook and Beyea 2000)
First and second generation biofuels	N.S.	Europe	Assessment of environmental impacts of energy crop cultivation	Land-use change, pesticide and fertilizer pollution, overexploitation of soils (loss in soil quality, erosion), pollution by wastes	N.S.	Reduction of biodiversity in monocultures. Potential increases in biodiversity when using second generation biofuels	(Fernando et al. 2010)

First and second generation biofuels	N.S.	Global	Assessment of biofuel sustainability potential in 2020	Land-use change (direct-indirect), greenhouse gas emissions	Natural lands, marginal lands	Habitat is expected to be lost as a result of biofuel and crop expansion for food production. Expected conflicts between available lands for competing objectives and expected increases in carbon emissions as a result of land-use change.	(Bindraban et al. 2009)
First and second generation biofuels	N.S.	Global	Review of the potential effects of biofuel production on ecosystems	Land-use change (direct, indirect), greenhouse gas emissions, overexploitation of soils (erosion, leaching of soil nutrients, continuous removal of agricultural residues), pesticide and fertilizer pollution, water depletion, invasive potential of biofuel crops	Agricultural lands, native ecosystems, marginal or degraded lands.	Habitat losses, potential habitat gains in marginal or degraded lands if replaced by second generation biofuels	(Bonin and Lal 2012)
First and second generation biofuels	N.S.	Global	Overview of current and potential environmental impacts of biofuel production	Land-use change, soil overexploitation, pesticide and fertilizer pollution, invasive potential, water depletion, greenhouse gas emissions	Native ecosystems and agricultural lands	Habitat losses, higher when biodiverse ecosystems are transformed into crops. Potential positive impacts if habitat heterogeneity is increased or land degradation is reversed	(Dauber and Bolte 2014)
First and second generation biofuels	N.S.	Global	Review of the ecological impacts of biofuels	Land-use change (direct-indirect), greenhouse gas emissions as a result of land-use change and indirect or market-mediated effects, air pollution, water depletion and pollution	Agricultural lands, abandoned lands, other uses including native forests and grasslands	Habitat can be lost both within and outside biofuel production areas, reduction in grassland areas in the USA, direct and indirect conversion of grasslands, shrublands and forests in Brazil, conversion of forests in Southeast Asia	(Fargione et al. 2010)
First and second generation biofuels	N.S.	Global	Overview of the prospects of future global crop sustainability to 2050	Land-use change (direct, indirect), land-use intensification, water depletion, increases in greenhouse gas emissions (climate change)	Agricultural lands, native ecosystems	Current and expected habitat losses as native ecosystems are transformed into biofuel crops	(Hertel 2015)
First and second generation biofuels	N.S.	Global	Review of trade-offs between ecosystem services and agriculture, including biofuel crops	Land-use change, greenhouse gas emissions	N.S.	Expected conflicts between biofuel production and ecosystem services, some of them related to changes in biodiversity (e.g. biological control)	(Power 2010)
First and second generation biofuels	N.S.	Global	Review of the assumptions for the estimation of global bioenergy potential	Land-use change, land-use intensification, water depletion	Agricultural lands, native ecosystems (e.g. natural grasslands)	Potential total habitat losses would depend on several assumptions, including type and productivity of feedstocks and type of land used for biofuel crops (e.g. surplus agricultural, lands, degraded lands)	(Slade et al. 2014)
First generation biofuels (Focus on sugarcane)	N.S.	Global (Focus on Brazil and Europe)	Overview of the synergies and trade-offs between biofuel production, food production and biodiversity conservation	Land-use change (direct, indirect), land-use intensification, water depletion, pesticide and fertilizer pollution, soil overexploitation, air pollution	Agricultural lands, natural, and semi-natural ecosystems	Habitat losses. Potential biodiversity improvements if current biofuel crops are better managed for improving biodiversity and ecosystem services, taking into account spatial arrangements.	(Manning et al. 2015)
First generation biofuels (mainly oil palm, soybean, sugarcane)	N.S.	Tropical region	Review of the environmental impacts of biofuel in biodiversity hotspots	Land-use change (direct, indirect), land-use intensification, greenhouse gas emissions, pesticide and fertilizer pollution, detrimental management practices (e.g. burning of sugarcane straw), soil overexploitation (soil erosion), pollution by wastes (e.g. palm oil mill effluent), increases in infrastructure, detrimental synergies with other industries (e.g. oil palm plantations and charcoal industries)	Agricultural lands, native ecosystems, degraded lands	Habitat losses, decreases in richness of species with high ecological requirements, biotic homogenization.	(Lee 2011)
First generation biofuels (oil palm)	Mammals (Orangutan)	Asia (Indonesia, Malaysia)	Assessment of the strategies that reduce the potential for orangutan conservation	Land-use change	Native forests	Habitat loss as a result of deforestation. If *Imperata* grasslands are used for oil palm plantations habitat loss could decrease.	(Nantha and Tisdell 2009)
First generation biofuels (oil palm)	N.S.	Asia (Indonesia)	Review of environmental and social impacts of biofuel production from oil palm	Land-use change, emission of air pollutants and other wastes, overexploitation of soils (soil erosion), water depletion, increases in greenhouse gas emissions when native ecosystems are transformed	Native ecosystems (rainforests, peatlands, secondary forests)	Loss of habitat for native species, decreases in richness and abundance of native and threatened species (e.g. Sumatran tiger, orangutan)	(Obidzinski et al. 2012)
First generation biofuels (oil palm)	N.S.	Asia (Southeast Asia)	Review and assessment of the sustainability of oil palm plantations in Southeast Asia	Land-use change, land-use intensification, overexploitation of soils (decreases in soil quality, increases in soil erosion), water depletion, emission of wastes, changes in ecological conditions (fire regimes)	Native ecosystems	Loss of habitat for native and threatened species	(Mukherjee and Sovacool 2014)
First generation biofuels (oil palm)	N.S.	Asia (Southeast Asia)	Review of potential solutions to decrease threats to biodiversity associated with oil palm expansion	Land-use change	Native forests	Habitat loss for native species	(Wilcove and Koh 2010)
First generation biofuels (oil palm)	N.S.	Tropical region	Review and meta-analysis of life cycle assessments for oil palm production	Land-use change, greenhouse gas emissions (potential of global warming), pesticide and fertilizer pollution, water depletion	Primary, secondary forests, agricultural lands, grasslands	Habitat loss for native species, species richness decreases in plantations, less impacts are expected when replacing agricultural lands or grasslands	(Manik and Halog 2013)
First generation biofuels (rapeseed, sunflower, oil palm, soybean)	N.S.	Global	Overview of the potential habitat and biodiversity losses from biofuel production	Land-use change, land-use intensification	Agricultural lands, native ecosystems	Current and potential habitat loss	(Koh 2007)
First generation biofuels (soybean and oil palm)	Mammals (Primates)	Global	Review of prospects and threats for primate conservation in the world	Land-use change, pesticide and fertilizer pollution, infrastructure development	Tropical forests	Current and potential habitat losses as a result of deforestation.	(Estrada 2013)

First generation biofuels (soybean) and beef tallow	N.S.	Americas (Brazil)	Review of the impacts and environmental sustainability of biodiesel production in Brazil	Land-use change (direct, indirect), greenhouse gas emissions (a result of land use-change, use of fertilizers, transportation activities), water depletion, pesticide and fertilizer pollution, overexploitation of soils (e.g. erosion)	Agricultural lands, native ecosystems (natural grasslands, forests)	Reported habitat losses mainly as a result of replacement of natural grasslands for soybean plantations. Indirect land-use change (deforestation) in the Amazon region.	(Castanheira et al. 2014)
First generation biofuels (sugarcane)	Birds, mammals	Americas (Brazil)	Review of environmental and economic aspects of ethanol production in Brazil	Land-use change (direct, indirect), land-use intensification, greenhouse gas emissions, water depletion, pollution by wastes (e.g. burning crop residues).	Agricultural lands, native ecosystems (including savannas and forests)	Habitat and biodiversity losses as a result of intensification and to a minor extent as a result of replacement of native habitats within the study region	(Walter et al. 2014)
First generation biofuels (sugarcane)	N.S.	Americas (Brazil)	Assessment of environmental impacts of sugarcane cropping	Land-use change, land-use intensification, greenhouse gas emissions, water depletion, overexploitation of soils (e.g. soil erosion), pesticide and fertilizer pollution, pollution by wastes (e.g. air pollution after bagasse is burned, water pollution when vinasses reach aquatic systems), direct and indirect climatic shifts (e.g. changes in temperature as a result of changes in albedo)	Agricultural lands, native grasslands, and forests	Habitat has been lost and is expected to continue (including fragmentation), biotic homogenization	(Filoso et al. 2015)
First generation biofuels (sugarcane)	N.S.	Americas (Brazil)	Review of environmental impacts of sugarcane production	Land-use change (direct-indirect), greenhouse gas emissions, soil erosion, water depletion and pollution, pesticide and fertilizer pollution, pollution by wastes (e.g. burning crop residues)	Agricultural lands (pastures, croplands) and native ecosystems including natural grasslands	Loss of habitat for native species if sugarcane expands into native ecosystems.	(Smeets et al. 2008)
First generation biofuels (sugarcane, soybean)	N.S.	Americas (Brazil)	Review of past and future land-use change impacts of biofuel production	Land-use change (direct, indirect), land-use intensification, greenhouse gas emissions	Agricultural lands, native ecosystems (including natural savannas, gallery forests, and Amazon forest)	Expected higher habitat losses in the future as a result of biofuel crop expansion	(Volpi 2010)
First generation biofuels (sugarcane, soybean, oil palm)	N.S.	Americas (Brazil)	Review of hazards imposed by current registered pesticides	Land-use change (direct, indirect), land-use intensification, pesticide and fertilizer pollution	Agricultural lands, native ecosystems (forests, native grasslands)	Habitat loss as native ecosystems are transformed into pastures and then into biofuel crops. Expected toxicities for wildlife as a result of increased use of pesticides	(Schiesari and Grillitsch 2011)
First, second (agricultural and forest residues, organic wastes) and third generation biofuels (microalgae)	N.S.	Global	Review of different biofuel production alternatives and their sustainability potential and deployment potential by 2050	Land-use change (direct, indirect), greenhouse gas emissions, overexploitation of soils (reduction of fertility as a result of continuous harvesting of residues), direct and indirect climate shifts (changes in albedo, roughness, evapotranspiration), pesticide and fertilizer pollution, water depletion	Agricultural land, marginal or degraded lands, native ecosystems	Habitat losses and high carbon emissions when native ecosystems are replaced, potential carbon losses in intensively managed forests for biomass extraction, habitat losses dependent on crop specific yields and management practices, habitat degradation. Use of degraded land for perennial plantations can increase biodiversity. Emission of air pollutants can be reduced (e.g. SOx and particulate matter)	(Creutzig et al. 2015)
First, second and third generation biofuels (microalgae)	Birds, mammals, amphibians, reptiles	Global	Review of impacts of biofuels production on biodiversity	Land-use change, land-use intensification, pesticide and fertilizer pollution, water depletion, increases in greenhouse gas emissions (global warming potential), changes in management regimes, potential invasive species, genetic pollution	Native ecosystems, agricultural lands	Habitat loss for native and threatened species, homogenization, alteration of species composition and species populations	(Liu et al. 2014)
First, second and third generation biofuels (microalgae)	Birds, mammals, amphibians, reptiles	Global	Review of environmental impacts of biofuel crops	Land-use change (direct, indirect), land-use intensification, pesticide and fertilizer pollution, invasive species, spread of diseases, water depletion	Agricultural lands, degraded lands, native ecosystems	Impacts on biodiversity are context dependent, although are mostly negative	(Verdade et al. 2015)
First, second and third generation biofuels (microalgae)	N.S.	Asia (Southeast Asia)	Overview of the social and environmental costs of biofuels in Asia	Land-use change (direct-indirect), greenhouse gas emissions as a result of land use change and management practices, water depletion, emissions of wastes, invasiveness potential	Agricultural lands, marginal lands, abandoned lands, native ecosystems including forests, grasslands and wetlands	Habitat loss for native species	(Phalan 2009)
First, second and third generation biofuels (microalgae)	N.S.	Global	Overview of the impacts of direct and indirect land-use change on greenhouse gas emissions	Land-use change (direct, indirect), greenhouse gas emissions	Native ecosystems, abandoned and degraded lands	Carbon losses when rich carbon systems are transformed into biofuel crops. Biodiversity losses may occur in marginal lands. Biofuel options that do not compete with other uses may be preferred (e.g. microalgal systems)	(Fritsche et al. 2010)
First, second and third generation biofuels (microalgae)	N.S.	Global	Review of the current debate on biofuel sustainability	Land-use change, land-use intensification, greenhouse gas emissions, pollution by wastes, pesticide and fertilizer pollution, overexploitation of soils (e.g. organic carbon losses, losses in soil fertility), water depletion, invasive potential	Agricultural lands, native ecosystems	Habitat losses, higher greenhouse emissions when transforming rich carbon ecosystems	(Gomiero 2015)
First, second and third generation biofuels (microalgae)	N.S.	Global	Assessment of biofuel production potential and its environmental impacts	Land-use change (direct-indirect), land-use intensification, greenhouse gas emissions as a result of land-use change, water depletion	Agricultural lands (including agroforest systems) and native ecosystems	Habitat loss for native species (e.g. orangutan in Southeast Asia)	(Koh and Ghazoul 2008)
First, second and third generation biofuels (microalgae)	N.S.	Global	Review about the environmental impacts of biofuels	Land-use change (direct-indirect), land-use intensification, greenhouse gas emissions (as a result of land-use change and production technologies), pesticide and fertilizer pollution, invasive species	Native ecosystems, semi-natural areas, agricultural and marginal lands	Less expected habitat losses for biofuel produced from wastes and from third generation biofuels. Potential biodiversity gains if landscape heterogeneity increases.	(Wiens et al. 2011)
First, second and third generation biofuels (microalgae)	N.S.	Oceania (Australia)	Quantitative assessment of current and future biofuel	Land-use change, greenhouse gas emissions, overexploitation of soils, water depletion	Agricultural and marginal lands	Potential positive impacts if saline and degraded lands are replaced by eucalypt forests	(Farine et al. 2012)

			crops and associated estimates of greenhouse gas mitigation				
First, second generation and third generation biofuels (microalgae)	N.S.	Global	Review of the opportunities of crops for food, feed and biofuel production	Land-use change, land-use intensification, greenhouse gas emissions, pesticide and fertilizer pollution	Agricultural lands, marginal lands, native ecosystems	Habitat and biodiversity losses depend on agroecological conditions, soil traits and cropping systems	(Spiertz and Ewert 2009)
N.S.	N.S.	Global	Assessment of surplus land availability for future biofuel expansion	Land-use change (direct-indirect), land-use intensification, potential increases in greenhouse gasses (as a result of carbon soil losses, energy intensive production technologies, fertilizers and distance to markets), pollution through fertilizers, increases in invasive species	"Surplus" lands including agricultural lands	Habitat loss for native species including those found in agricultural lands. Potential biodiversity gains if structural and functional heterogeneity increases.	(Dauber et al. 2012)
N.S.	N.S.	Global	Assessment of the impacts of climate change on biodiversity including the role of the potential expansion of biofuel crops	Land-use change (direct, indirect), land-use intensification, greenhouse gas emissions (climate change), soil overexploitation (e.g. soil erosion), pesticide and fertilizer pollution, water depletion	Agricultural lands, marginal lands, native ecosystems	Expected habitat losses within and outside Europe for fulfilling European biodiesel demands	(Omann et al. 2009)
N.S.	N.S.	Tropical region	Review of strategies for potential reduction of synergistic threats on biodiversity	Land-use change (direct-indirect) , greenhouse gasses emissions as a result of land-use change	Tropical forests	Habitat loss and disturbance for native species	(Brodie et al. 2012)
N.S.	N.S.	Tropical region	Review of emerging threats to tropical forests	Land-use change (direct, indirect), land-use intensification	Tropical forests	Habitat loss for native and threatened species	(Laurance 2015)
N.S.	N.S.	Tropical region	Assessment of future of forests based on threats for biodiversity conservation	Land-use change, land-use intensification,	Tropical forests	Loss of habitat for native and threatened species, increases in forest degradation	(Putz and Romero 2014)
Second and third generation biofuels (microalgae)	N.S.	N.S. for the microalgal systems. Boreal forest for the forest system	Overview of life cycle assessment comparing lignocellulosic biofuels with microalgal systems	Land-use change (direct, indirect), greenhouse gas emissions, water depletion, soil overexploitation (e.g. decreases in soil fertility and changes in texture), pesticide and fertilizer pollution, introduction of invasive species, genetic pollution	Managed forests, non-arable land	Expected fewer habitat losses when using microalgal systems	(Holma et al. 2013)
Third generation biofuels (microalgae)	N.S.	Global	Review of the potential environmental risks of microalgal biofuel production	Land-use change, water depletion, greenhouse gas emissions, pollution through wastes (e.g. water pollution by fertilizer and chemical use), invasive species, genetic pollution (by leakages of genetically modified algae), soil overexploitation (soil pollution, soil erosion)	N.S.	Potential changes in biodiversity as a result of land-use change and water pollution	(Zhu and Ketola 2012)
Third generation biofuels (microalgae)	N.S.	Global	Exploration of sustainability aspects of microalgal biorefinery systems	Land-use change, water depletion, pollution by wastes (i.e. wastewater), soil overexploitation (soil erosion, soil compaction), invasive species, greenhouse gas emissions	Marginal lands (e.g. arid or saline soils, infertile or polluted lands)	Potential biodiversity losses	(Zhu et al. 2015)
Third generation biofuels (microalgae)	N.S.	Global	Overview of the potential environmental impacts of large-scale microalgal cultivation	Land-use change, pollution by wastes (wastewater), water depletion, invasive species	Marginal lands, forested areas, pastures	Potential habitat losses and changes in terrestrial and aquatic ecosystems. Some species could make use of ponds for drinking water.	(Usher et al. 2014)

2. Calculation of area needed to satisfy gasoline and distillate fuel oil demands in 2010

Tables S3 and S4 list the selected crops that may be used for biodiesel and bioethanol production, based on their lipid and carbohydrate contents, respectively. Average biodiesel yields per crop within countries was calculated based on the following equation:

$BDY = CY*LP/OD*0.81$

Where BDY is average biodiesel yield per crop within countries (L ha^{-1} year^{-1}), CY is the average crop yield between 2005 and 2014 for each country (tonnes ha^{-1} year^{-1}) (FAO 2019), LP is the proportion of lipids in the seeds, OD is oil density (tonnes L^{-1}), and 0.81 is the product of the assumed extraction efficiency of oils (0.9) and the conversion efficiency from lipids to biodiesel (0.9).

Average bioethanol yield per crop within countries was based on the following equation:

$ETY = CY*CE$

Where ETY is average bioethanol yield per crop within countries (L ha^{-1} year^{-1}), CY is the average crop yield between 2005 and 2014 for each country (tonnes ha^{-1} year^{-1}) (FAO 2019) and CE is the reported conversion efficiency per crop (L tonnes^{-1})

An area-weighted average was calculated for microalgal biodiesel yield per country, using the estimations from Moody et al. (2014), taking into account the mean value at lipid yield intervals of 550 L ha^{-1} year^{-1} and the proportion of land that these intervals represent within each country. Total average biodiesel yield was obtained multiplying by 0.81, which is the product of the assumed extraction efficiency of oils (0.9) and the conversion efficiency from lipids to biodiesel (0.9).

Average energy yields (GJ ha^{-1} year^{-1}) were obtained by multiplying the average biodiesel yields (L ha^{-1} year^{-1}) by 0.0326 GJ L^{-1}, using the Low Heating Value conversion factor. For bioethanol, a conversion factor of 0.0211 GJ L^{-1} was used (Hofstrand 2008).

Annual consumption of gasoline and distillate fuel oil within countries was obtained from the U.S. Energy Information Administration database (U.S. Energy Information Administration 2016). The amount of total energy consumption was obtained using a conversion factor at Low Heating Value of 5.113 GJ per barrel of gasoline and 5.703 GJ per barrel of distillate oil.

Finally, the amount of cultivation land required to meet gasoline and distillate fuel oil demands for each country in 2010 was obtained by dividing the annual consumption of gasoline and distillate fuel oil in 2010 (GJ year^{-1}) by their associated average energy yields (GJ ha^{-1} year^{-1}) (Tables S5 and S6).

Figures S1 to S5 and tables S7 to S11 show the cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010 using soybean, oil palm, and rapeseed for biodiesel, and maize and sugarcane for bioethanol, in comparison to microalgae.

Table S3. Conversion efficiencies for the production of biodiesel from selected crops found in the Faostat3 database. Averages of seed oil percentages were obtained from El Bassam (2010), tables 10.2 and 6.3; and averages of oil densities (at 15–25°C) were obtained from Firestone (2013).

Crops	Seed oil percentage	Oil density (Kg m^{-3})
Castor oil seed	50	956
Coconuts	36	921
Groundnuts, with shell	50	917
Hempseed	32	925
Jojoba seed	52	864
Linseed	39	930
Oil, palm fruit	26	920
Olives	40	910
Poppy seed	47	919
Rapeseed	45	910
Safflower seed	34	922
Sesame seed	55	915
Soybeans	21	919
Sunflower seed	43	918
Tallowtree seed	19	939

Table S4. Conversion efficiencies for the production of ethanol from selected crops found in the Faostat3 database. Efficiency conversion refers to the amount of produced ethanol in liters per tonne of feedstock.

Crops	Efficiency conversion (L tonne^{-1})	Reference
Barley	371	El Bassam (2010), table 10.1
Cassava	322	El Bassam (2010), table 10.1
Maize	417	El Bassam (2010), table 10.1
Oats	317	El Bassam (2010), table 11.1
Potatoes	114	El Bassam (2010), table 10.1
Rice, paddy	430	Rajagopal et al. (2007)
Rye	360	Wang et al. (1997)
Sorghum	380	Rajagopal et al. (2007)
Sugar beet	110	Rajagopal et al. (2007)
Sugarcane	83	de Vries et al. (2010)
Sweet potatoes	200	El Bassam (2010), table 10.1
Triticale	382	El Bassam (2010), table 11.1
Wheat	396	El Bassam (2010), table 10.1

Table S5. Cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, for the best biodiesel crop in comparison to microalgal systems. Relative cultivation area of microalgal systems in comparison to best biodiesel crop is showed.

Country	Best biodiesel crop	Area (km^2) for best biodiesel crop	Area (km^2) for microalgae	Relative cultivation area of microalgal systems (%)
Afghanistan	Olives	26,150.1	1,650.1	6.3
Albania	Sunflower seed	14,709.8	811.9	5.5
Algeria	Rapeseed	150,194.3	8,747.7	5.8
American Samoa	Coconuts	2,606.6	126.2	4.8
Angola	Oil, palm fruit	17,795.7	2,663.3	15.0
Argentina	Groundnuts, with shell	200,584.8	16,235.9	8.1
Australia	Groundnuts, with shell	421,362.1	22,653.9	5.4
Austria	Rapeseed	98,358.3	13,493.5	13.7
Azerbaijan	Sunflower seed	41,837.7	2,166.2	5.2
Bahamas	Coconuts	2,621.2	377.5	14.4
Bangladesh	Groundnuts, with shell	55,295.2	2,362.8	4.3
Barbados	Groundnuts, with shell	1,803.0	153.1	8.5
Belarus	Rapeseed	102,608.2	7,066.9	6.9
Belgium	Rapeseed	108,949.2	21,891.3	20.1
Belize	Coconuts	1,507.4	87.8	5.8
Benin	Oil, palm fruit	3,914.9	810.7	20.7
Bhutan	Soybeans	4,886.6	78.2	1.6
Bolivia	Groundnuts, with shell	45,867.5	1,476.8	3.2
Bosnia and Herzegovina	Rapeseed	17,236.8	1,349.7	7.8
Botswana	Sunflower seed	26,436.7	590.2	2.2
Brazil	Coconuts	225,314.5	45,995.8	20.4
Brunei	Coconuts	13,217.1	408.3	3.1
Bulgaria	Rapeseed	34,895.3	2,801.9	8.0
Burkina Faso	Groundnuts, with shell	16,152.4	321.8	2.0
Burundi	Oil, palm fruit	294.5	36.5	12.4
Cambodia	Coconuts	6,105.1	625.1	10.2
Cameroon	Oil, palm fruit	3,084.0	789.7	25.6
Canada	Rapeseed	1,059,209.8	136,433.0	12.9
Cape Verde	Coconuts	840.4	48.8	5.8
Central African Republic	Oil, palm fruit	332.4	33.6	10.1
Chad	Groundnuts, with shell	1,918.5	39.5	2.1
Chile	Olives	79,750.6	10,181.4	12.8
China	Coconuts	895,340.0	276,923.3	30.9
Colombia	Oil, palm fruit	23,322.3	6,289.9	27.0
Comoros	Coconuts	469.7	22.5	4.8
Cook Islands	Coconuts	373.2	18.2	4.9
Costa Rica	Oil, palm fruit	5,996.7	1,287.4	21.5
Côte d'Ivoire	Coconuts	6,695.0	597.0	8.9
Croatia	Rapeseed	29,681.1	2,977.8	10.0
Cuba	Coconuts	16,953.2	1,175.0	6.9
Cyprus	Groundnuts, with shell	1,959.8	888.7	45.3
Czech Republic	Rapeseed	62,947.6	9,109.8	14.5
Democratic Republic of the Congo	Oil, palm fruit	4,487.2	372.0	8.3
Denmark	Rapeseed	52,328.8	10,328.2	19.7
Dominica	Coconuts	524.9	28.5	5.4
Dominican Republic	Oil, palm fruit	8,444.6	1,647.7	19.5
East Timor	Groundnuts, with shell	1,484.5	44.9	3.0
Ecuador	Oil, palm fruit	31,608.4	5,391.9	17.1
Egypt	Olives	67,976.3	12,605.4	18.5

El Salvador	Coconuts	3,635.0	779.4	21.4
Equatorial Guinea	Oil, palm fruit	954.2	128.7	13.5
Eritrea	Groundnuts, with shell	6,385.9	118.8	1.9
Estonia	Rapeseed	17,298.1	1,488.5	8.6
Ethiopia	Groundnuts, with shell	29,637.6	896.2	3.0
Fiji	Coconuts	3,048.8	190.8	6.3
Finland	Rapeseed	142,407.0	11,557.3	8.1
France	Hempseed	371,001.7	74,430.1	20.1
French Guiana	Coconuts	1,376.6	129.4	9.4
French Polynesia	Coconuts	2,048.0	148.4	7.2
Gabon	Oil, palm fruit	4,903.4	396.5	8.1
Gambia	Oil, palm fruit	753.3	98.2	13.0
Georgia	Soybeans	17,099.4	889.6	5.2
Germany	Rapeseed	632,743.3	117,604.2	18.6
Ghana	Coconuts	7,958.1	1,329.7	16.7
Greece	Sesame seed	16,009.0	9,726.2	60.8
Grenada	Coconuts	836.6	53.7	6.4
Guadeloupe	Coconuts	6,352.6	295.8	4.7
Guam	Coconuts	812.6	88.8	10.9
Guatemala	Oil, palm fruit	6,541.5	1,680.8	25.7
Guinea	Coconuts	1,882.3	130.0	6.9
Guinea-Bissau	Oil, palm fruit	389.5	43.0	11.0
Guyana	Coconuts	3,186.9	268.0	8.4
Haiti	Coconuts	8,148.5	419.1	5.1
Honduras	Oil, palm fruit	4,126.3	870.2	21.1
Hungary	Rapeseed	59,186.1	5,982.1	10.1
India	Coconuts	578,183.3	59,125.7	10.2
Indonesia	Oil, palm fruit	149,733.7	36,416.5	24.3
Iran	Groundnuts, with shell	517,215.3	38,078.9	7.4
Iraq	Groundnuts, with shell	150,905.6	12,945.3	8.6
Ireland	Rapeseed	42,900.0	8,813.8	20.5
Israel	Groundnuts, with shell	21,231.9	4,403.6	20.7
Italy	Sesame seed	100,818.9	44,140.6	43.8
Jamaica	Coconuts	7,030.3	691.4	9.8
Japan	Groundnuts, with shell	1,056,153.6	108,241.5	10.2
Jordan	Olives	44,211.8	2,082.3	4.7
Kazakhstan	Groundnuts, with shell	123,883.4	8,466.4	6.8
Kenya	Groundnuts, with shell	33,572.8	1,340.8	4.0
Kiribati	Coconuts	113.3	11.6	10.2
Kuwait	Olives	120,505.9	4,468.5	3.7
Kyrgyzstan	Groundnuts, with shell	14,661.2	854.6	5.8
Laos	Groundnuts, with shell	798.8	47.7	6.0
Latvia	Rapeseed	19,678.9	2,029.7	10.3
Lebanon	Groundnuts, with shell	30,661.8	3,205.6	10.5
Liberia	Oil, palm fruit	584.8	82.4	14.1
Libya	Groundnuts, with shell	134,894.8	7,373.5	5.5
Lithuania	Rapeseed	8,651.4	824.3	9.5
Luxembourg	Rapeseed	22,559.3	3,666.1	16.3
Macedonia	Rapeseed	7,424.9	569.9	7.7
Madagascar	Oil, palm fruit	2,019.6	313.5	15.5
Malawi	Groundnuts, with shell	6,884.7	162.3	2.4
Malaysia	Oil, palm fruit	48,182.3	14,884.0	30.9
Maldives	Coconuts	3,055.0	228.6	7.5
Mali	Groundnuts, with shell	4,206.0	126.2	3.0
Malta	Olives	20,401.9	456.7	2.2

Martinique	Coconuts	6,383.8	231.6	3.6
Mauritania	Groundnuts, with shell	15,605.1	320.0	2.1
Mauritius	Groundnuts, with shell	5,501.3	332.0	6.0
Mexico	Oil, palm fruit	238,950.8	42,614.4	17.8
Moldova	Rapeseed	14,704.5	819.8	5.6
Mongolia	Rapeseed	15,708.1	1,187.6	7.6
Montenegro	Olives	9,142.2	256.2	2.8
Morocco	Groundnuts, with shell	64,953.8	4,152.2	6.4
Mozambique	Coconuts	7,602.0	490.5	6.5
Myanmar	Coconuts	4,239.4	884.7	20.9
Namibia	Sunflower seed	26,859.9	639.0	2.4
Nauru	Coconuts	49.7	7.7	15.5
Nepal	Coconuts	6,463.9	636.7	9.8
Netherlands	Rapeseed	118,787.2	22,275.5	18.8
New Caledonia	Coconuts	1,820.9	216.9	11.9
New Zealand	Linseed	108,202.7	5,583.8	5.2
Nicaragua	Oil, palm fruit	1,669.2	469.0	28.1
Niger	Sesame seed	10,532.5	152.8	1.5
Nigeria	Coconuts	58,562.6	6,716.3	11.5
Niue	Coconuts	45.8	0.8	1.8
North Korea	Soybeans	25,735.5	580.0	2.3
Norway	Rapeseed	112,313.7	12,947.3	11.5
Pakistan	Coconuts	56,316.5	7,632.0	13.6
Palestina	Poppy seed	1,670.7	517.0	30.9
Panama	Oil, palm fruit	7,746.8	1,045.4	13.5
Papua New Guinea	Oil, palm fruit	1,931.1	377.1	19.5
Paraguay	Oil, palm fruit	7,547.2	1,001.0	13.3
Peru	Coconuts	17,634.4	4,730.6	26.8
Philippines	Oil, palm fruit	45,276.0	7,560.3	16.7
Poland	Rapeseed	205,424.3	26,993.4	13.1
Portugal	Groundnuts, with shell	98,092.1	6,705.8	6.8
Puerto Rico	Coconuts	7,887.6	2,268.8	28.8
Republic of Congo	Oil, palm fruit	2,135.3	348.9	16.3
Reunion	Coconuts	3,889.3	330.5	8.5
Romania	Rapeseed	100,371.9	7,130.0	7.1
Russia	Rapeseed	1,693,756.3	125,951.9	7.4
Rwanda	Rapeseed	6,100.3	99.4	1.6
Saint Kitts and Nevis	Coconuts	519.0	50.8	9.8
Saint Lucia	Coconuts	1,174.6	92.9	7.9
Saint Vincent and the Grenadines	Coconuts	679.0	44.7	6.6
Samoa	Coconuts	293.3	35.8	12.2
Sao Tome and Principe	Oil, palm fruit	169.0	22.1	13.1
Saudi Arabia	Groundnuts, with shell	357,869.5	36,038.8	10.1
Senegal	Oil, palm fruit	4,400.9	611.1	13.9
Serbia	Rapeseed	25,151.4	2,383.4	9.5
Seychelles	Coconuts	1,916.5	151.1	7.9
Sierra Leone	Oil, palm fruit	1,103.5	117.5	10.6
Singapore	Coconuts	18,815.2	3,708.2	19.7
Slovakia	Rapeseed	30,219.6	3,155.2	10.4
Slovenia	Rapeseed	28,375.3	3,071.3	10.8
Solomon Islands	Oil, palm fruit	216.8	47.3	21.8
Somalia	Coconuts	1,655.8	95.7	5.8
South Africa	Groundnuts, with shell	372,357.2	14,494.9	3.9
South Korea	Groundnuts, with shell	348,534.9	35,056.7	10.1

Spain	Groundnuts, with shell	366,344.6	38,059.4	10.4
Sri Lanka	Coconuts	18,882.6	1,877.9	9.9
Suriname	Coconuts	1,694.7	302.5	17.9
Swaziland	Groundnuts, with shell	12,017.4	155.1	1.3
Sweden	Rapeseed	102,640.4	16,546.3	16.1
Switzerland	Rapeseed	100,848.7	14,023.0	13.9
Syria	Groundnuts, with shell	78,978.2	6,401.4	8.1
Taiwan	Coconuts	47,672.7	12,032.8	25.2
Tajikistan	Groundnuts, with shell	3,765.4	297.1	7.9
Tanzania	Oil, palm fruit	4,126.9	737.6	17.9
Thailand	Oil, palm fruit	67,481.7	17,837.0	26.4
Togo	Oil, palm fruit	3,609.3	417.6	11.6
Tonga	Coconuts	130.0	33.0	25.4
Trinidad and Tobago	Coconuts	7,685.6	841.7	11.0
Tunisia	Linseed	41,853.1	1,821.8	4.4
Turkey	Groundnuts, with shell	142,744.7	16,833.9	11.8
Uganda	Sunflower seed	28,227.1	629.9	2.2
Ukraine	Rapeseed	175,425.6	13,791.7	7.9
United Kingdom	Rapeseed	417,125.7	78,255.1	18.8
United States	Olives	3,028,611.2	716,924.0	23.7
Uruguay	Rapeseed	22,577.6	1,296.3	5.7
Uzbekistan	Sunflower seed	43,732.9	2,574.2	5.9
Vanuatu	Coconuts	477.3	30.4	6.4
Venezuela	Coconuts	92,496.1	17,659.3	19.1
Vietnam	Coconuts	54,354.9	10,683.5	19.7
Yemen	Sesame seed	115,421.5	3,272.7	2.8
Zambia	Soybeans	17,114.3	324.2	1.9
Zimbabwe	Soybeans	27,018.8	409.0	1.5

Table S6. Cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, for the best bioethanol crop in comparison to microalgal systems. Relative cultivation area of microalgal systems in comparison to best bioethanol crop is showed.

Country	Best Ethanol crop	Area (km^2) for best ethanol crop	Area (km^2) for microalgae	Relative cultivation area of microalgal systems (%)
Afghanistan	Sugarcane	17,785.5	1,650.1	9.3
Albania	Potatoes	6,275.8	811.9	12.9
Algeria	Sorghum	70,870.9	8,747.7	12.3
American Samoa	Cassava	1,615.3	126.2	7.8
Angola	Cassava	18,367.9	2,663.3	14.5
Antigua and Barbuda	Cassava	1,258.3	74.8	5.9
Argentina	Sugarcane	60,132.9	16,235.9	27.0
Armenia	Maize	2,890.5	351.4	12.2
Australia	Sugarcane	91,133.2	22,653.9	24.9
Austria	Sugar beet	25,094.1	13,493.5	53.8
Azerbaijan	Sugar beet	12,815.3	2,166.2	16.9
Bahamas	Cassava	1,934.4	377.5	19.5
Bahrain	Potatoes	10,804.4	740.5	6.9
Bangladesh	Sugarcane	17,211.9	2,362.8	13.7
Barbados	Cassava	630.5	153.1	24.3
Belarus	Sugar beet	20,328.0	7,066.9	34.8
Belgium	Sugar beet	32,683.3	21,891.3	67.0
Belize	Cassava	478.8	87.8	18.3
Benin	Cassava	4,668.6	810.7	17.4

Bermuda	Potatoes	584.3	64.5	11.0
Bhutan	Sugarcane	613.1	78.2	12.8
Bolivia	Sugarcane	9,319.9	1,476.8	15.8
Bosnia and Herzegovina	Sugar beet	10,770.7	1,349.7	12.5
Botswana	Wheat	34,294.7	590.2	1.7
Brazil	Sugarcane	188,711.3	45,995.8	24.4
Brunei	Cassava	1,928.9	408.3	21.2
Bulgaria	Rice, paddy	20,951.5	2,801.9	13.4
Burkina Faso	Sugarcane	1,017.9	321.8	31.6
Burundi	Sugarcane	193.4	36.5	18.9
Cambodia	Cassava	2,123.1	625.1	29.4
Cameroon	Cassava	4,934.1	789.7	16.0
Canada	Sugar beet	192,510.8	136,433.0	70.9
Cape Verde	Cassava	346.6	48.8	14.1
Cayman Islands	Cassava	2,675.7	122.6	4.6
Central African Republic	Cassava	1,003.2	33.6	3.4
Chad	Sugarcane	133.4	39.5	29.6
Chile	Sugar beet	20,478.0	10,181.4	49.7
China	Sugarcane	769,456.6	276,923.3	36.0
Colombia	Sugarcane	21,516.6	6,289.9	29.2
Comoros	Cassava	321.4	22.5	7.0
Cook Islands	Cassava	55.9	18.2	32.6
Costa Rica	Sugarcane	5,530.9	1,287.4	23.3
Côte d'Ivoire	Sugarcane	2,612.7	597.0	22.9
Croatia	Sugar beet	8,580.3	2,977.8	34.7
Cuba	Sugarcane	11,044.1	1,175.0	10.6
Cyprus	Potatoes	7,934.7	888.7	11.2
Czech Republic	Sugar beet	18,586.5	9,109.8	49.0
Democratic Republic of the Congo	Sugarcane	2,939.7	372.0	12.7
Denmark	Sugar beet	18,075.9	10,328.2	57.1
Djibouti	Maize	2,317.2	57.6	2.5
Dominica	Cassava	302.6	28.5	9.4
Dominican Republic	Sugarcane	10,512.5	1,647.7	15.7
East Timor	Cassava	971.8	44.9	4.6
Ecuador	Sugarcane	20,468.2	5,391.9	26.3
Egypt	Sugarcane	35,047.3	12,605.4	36.0
El Salvador	Sugarcane	3,017.8	779.4	25.8
Equatorial Guinea	Sweet potatoes	3,403.1	128.7	3.8
Eritrea	Barley	7,975.9	118.8	1.5
Estonia	Potatoes	9,544.9	1,488.5	15.6
Ethiopia	Sugarcane	2,772.5	896.2	32.3
Faroe Islands	Potatoes	1,735.8	376.6	21.7
Fiji	Cassava	1,314.6	190.8	14.5
Finland	Sugar beet	27,774.1	11,557.3	41.6
France	Sugar beet	118,439.8	74,430.1	62.8
French Guiana	Sugarcane	668.5	129.4	19.4
French Polynesia	Sugarcane	621.4	148.4	23.9
Gabon	Sugarcane	2,149.2	396.5	18.4
Gambia	Cassava	2,377.2	98.2	4.1
Georgia	Potatoes	12,479.8	889.6	7.1
Germany	Sugar beet	204,170.3	117,604.2	57.6
Ghana	Cassava	7,154.5	1,329.7	18.6
Greece	Sugar beet	29,724.9	9,726.2	32.7
Grenada	Sugarcane	389.6	53.7	13.8

Guadeloupe	Sugarcane	1,609.6	295.8	18.4
Guam	Sweet potatoes	961.8	88.8	9.2
Guatemala	Sugarcane	5,848.9	1,680.8	28.7
Guinea	Sugarcane	773.3	130.0	16.8
Guinea-Bissau	Cassava	381.5	43.0	11.3
Guyana	Sugarcane	1,361.0	268.0	19.7
Haiti	Sugarcane	2,153.6	419.1	19.5
Honduras	Sugarcane	3,457.5	870.2	25.2
Hong Kong	Sweet potatoes	51,076.4	5,945.1	11.6
Hungary	Sugar beet	14,877.7	5,982.1	40.2
Iceland	Potatoes	5,030.8	1,304.1	25.9
India	Cassava	135,108.4	59,125.7	43.8
Indonesia	Cassava	149,214.6	36,416.5	24.4
Iran	Sugarcane	151,936.5	38,078.9	25.1
Iraq	Potatoes	183,553.5	12,945.3	7.1
Ireland	Sugar beet	19,909.6	8,813.8	44.3
Israel	Maize	11,381.1	4,403.6	38.7
Italy	Sugar beet	132,754.4	44,140.6	33.2
Jamaica	Cassava	3,135.4	691.4	22.1
Japan	Sugar beet	261,293.1	108,241.5	41.4
Jordan	Maize	6,835.4	2,082.3	30.5
Kazakhstan	Sugar beet	55,323.5	8,466.4	15.3
Kenya	Sugarcane	5,665.5	1,340.8	23.7
Kuwait	Maize	8,924.8	4,468.5	50.1
Kyrgyzstan	Maize	6,080.6	854.6	14.1
Laos	Cassava	168.4	47.7	28.3
Latvia	Sugar beet	6,208.8	2,029.7	32.7
Lebanon	Sugar beet	15,932.6	3,205.6	20.1
Lesotho	Potatoes	1,317.6	100.0	7.6
Liberia	Cassava	902.8	82.4	9.1
Libya	Potatoes	88,207.8	7,373.5	8.4
Lithuania	Sugar beet	2,008.8	824.3	41.0
Luxembourg	Potatoes	13,362.4	3,666.1	27.4
Macedonia	Sugar beet	3,363.2	569.9	16.9
Madagascar	Sugarcane	3,152.1	313.5	9.9
Malawi	Sugarcane	498.9	162.3	32.5
Malaysia	Cassava	61,442.6	14,884.0	24.2
Maldives	Maize	3,753.4	228.6	6.1
Mali	Sugarcane	553.9	126.2	22.8
Malta	Potatoes	4,488.1	456.7	10.2
Martinique	Sugarcane	1,484.7	231.6	15.6
Mauritania	Rice, paddy	3,913.8	320.0	8.2
Mauritius	Sugarcane	1,479.9	332.0	22.4
Mexico	Sugarcane	182,604.8	42,614.4	23.3
Moldova	Sugar beet	3,935.7	819.8	20.8
Mongolia	Potatoes	12,147.9	1,187.6	9.8
Montenegro	Maize	2,813.8	256.2	9.1
Montserrat	Maize	200.1	18.5	9.2
Morocco	Sugar beet	16,999.7	4,152.2	24.4
Mozambique	Sugarcane	2,327.7	490.5	21.1
Myanmar	Sugarcane	4,072.2	884.7	21.7
Namibia	Wheat	7,065.7	639.0	9.0
Nepal	Sugarcane	3,889.7	636.7	16.4
Netherlands	Sugar beet	32,675.5	22,275.5	68.2
New Caledonia	Cassava	2,696.8	216.9	8.0

New Zealand	Potatoes	18,336.6	5,583.8	30.5
Nicaragua	Sugarcane	1,685.9	469.0	27.8
Niger	Cassava	778.4	152.8	19.6
Nigeria	Cassava	53,643.7	6,716.3	12.5
Niue	Sweet potatoes	6.7	0.8	12.3
North Korea	Sweet potatoes	3,192.5	580.0	18.2
Norway	Potatoes	42,889.3	12,947.3	30.2
Oman	Sorghum	11,623.2	2,482.9	21.4
Pakistan	Sugarcane	41,722.3	7,632.0	18.3
Palestina	Sweet potatoes	2,537.5	517.0	20.4
Panama	Sugarcane	5,504.3	1,045.4	19.0
Papua New Guinea	Cassava	2,834.3	377.1	13.3
Paraguay	Cassava	5,361.8	1,001.0	18.7
Peru	Sugarcane	11,226.1	4,730.6	42.1
Philippines	Sugarcane	27,523.7	7,560.3	27.5
Poland	Sugar beet	59,822.7	26,993.4	45.1
Portugal	Sugarcane	19,832.2	6,705.8	33.8
Puerto Rico	Cassava	23,310.2	2,268.8	9.7
Qatar	Maize	13,643.6	3,159.2	23.2
Republic of Congo	Sugarcane	2,991.8	348.9	11.7
Reunion	Sweet potatoes	1,303.8	330.5	25.3
Romania	Sugar beet	30,251.7	7,130.0	23.6
Russia	Sugar beet	334,361.7	125,951.9	37.7
Rwanda	Cassava	790.1	99.4	12.6
Saint Kitts and Nevis	Sugarcane	306.3	50.8	16.6
Saint Lucia	Sweet potatoes	1,261.0	92.9	7.4
Saint Vincent and the Grenadines	Maize	152.6	44.7	29.3
Samoa	Cassava	220.4	35.8	16.2
Sao Tome and Principe	Cassava	424.0	22.1	5.2
Saudi Arabia	Potatoes	340,323.2	36,038.8	10.6
Senegal	Sugarcane	1,733.0	611.1	35.3
Serbia	Sugar beet	7,772.6	2,383.4	30.7
Seychelles	Cassava	1,032.9	151.1	14.6
Sierra Leone	Sugarcane	534.2	117.5	22.0
Slovakia	Sugar beet	7,340.0	3,155.2	43.0
Slovenia	Sugar beet	9,414.1	3,071.3	32.6
Solomon Islands	Cassava	222.3	47.3	21.3
Somalia	Cassava	949.7	95.7	10.1
South Africa	Sugarcane	73,281.8	14,494.9	19.8
South Korea	Sweet potatoes	176,396.3	35,056.7	19.9
Spain	Sugar beet	88,177.3	38,059.4	43.2
Sri Lanka	Sugarcane	10,478.7	1,877.9	17.9
Suriname	Cassava	987.5	302.5	30.6
Swaziland	Sugarcane	499.1	155.1	31.1
Sweden	Sugar beet	28,508.0	16,546.3	58.0
Switzerland	Sugar beet	23,094.6	14,023.0	60.7
Syria	Sugar beet	28,286.7	6,401.4	22.6
Taiwan	Cassava	36,025.4	12,032.8	33.4
Tajikistan	Maize	1,476.0	297.1	20.1
Tanzania	Sugarcane	3,607.5	737.6	20.4
Thailand	Cassava	62,355.8	17,837.0	28.6
Togo	Cassava	6,250.9	417.6	6.7
Tonga	Cassava	180.2	33.0	18.3
Trinidad and Tobago	Sugarcane	5,083.8	841.7	16.6

Tunisia	Sugar beet	7,888.5	1,821.8	23.1
Turkey	Sugar beet	60,379.8	16,833.9	27.9
Turkmenistan	Sugar beet	49,352.9	2,913.2	5.9
Uganda	Sugarcane	3,193.0	629.9	19.7
Ukraine	Sugar beet	54,131.5	13,791.7	25.5
United Arab Emirates	Sorghum	9,027.9	7,097.8	78.6
United Kingdom	Sugar beet	122,722.2	78,255.1	63.8
United States	Sugar beet	1,755,095.8	716,924.0	40.8
Uruguay	Sugarcane	6,706.1	1,296.3	19.3
Uzbekistan	Maize	15,211.1	2,574.2	16.9
Vanuatu	Maize	3,280.2	30.4	0.9
Venezuela	Sugarcane	78,495.3	17,659.3	22.5
Vietnam	Cassava	43,560.5	10,683.5	24.5
Western Sahara	Barley	5,077.9	41.4	0.8
Yemen	Sweet potatoes	53,185.6	3,272.7	6.2
Zambia	Sugarcane	1,053.7	324.2	30.8
Zimbabwe	Sugarcane	1,766.8	409.0	23.1

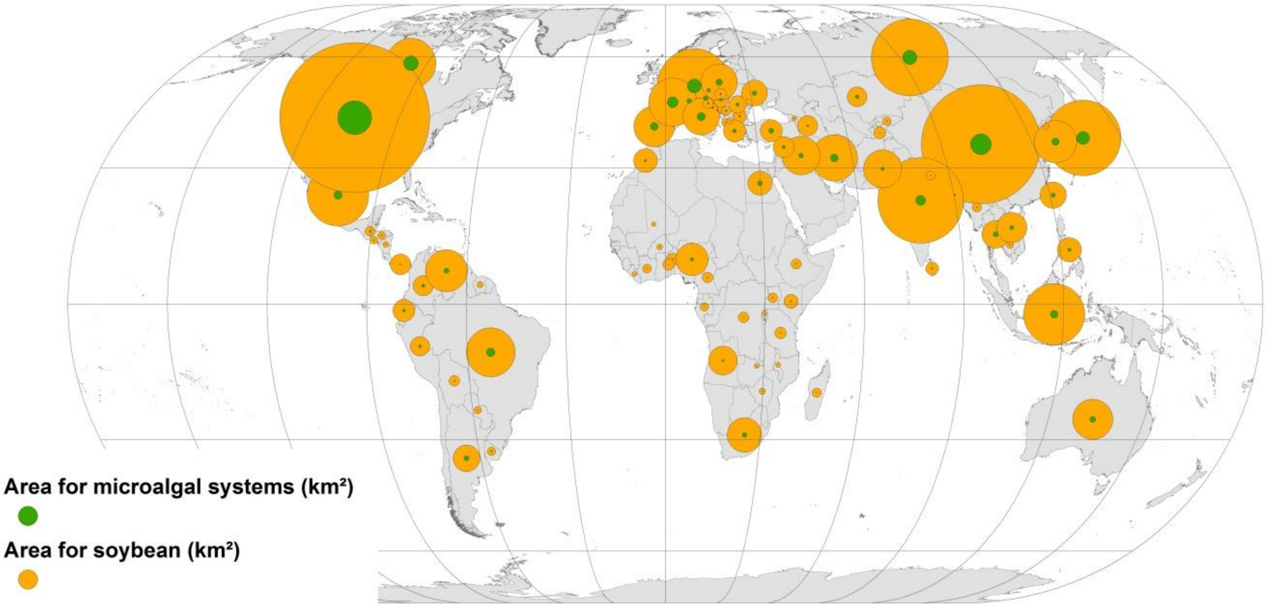

Figure S1. Superimposed circles showing the cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, when comparing microalgae with soybean production.

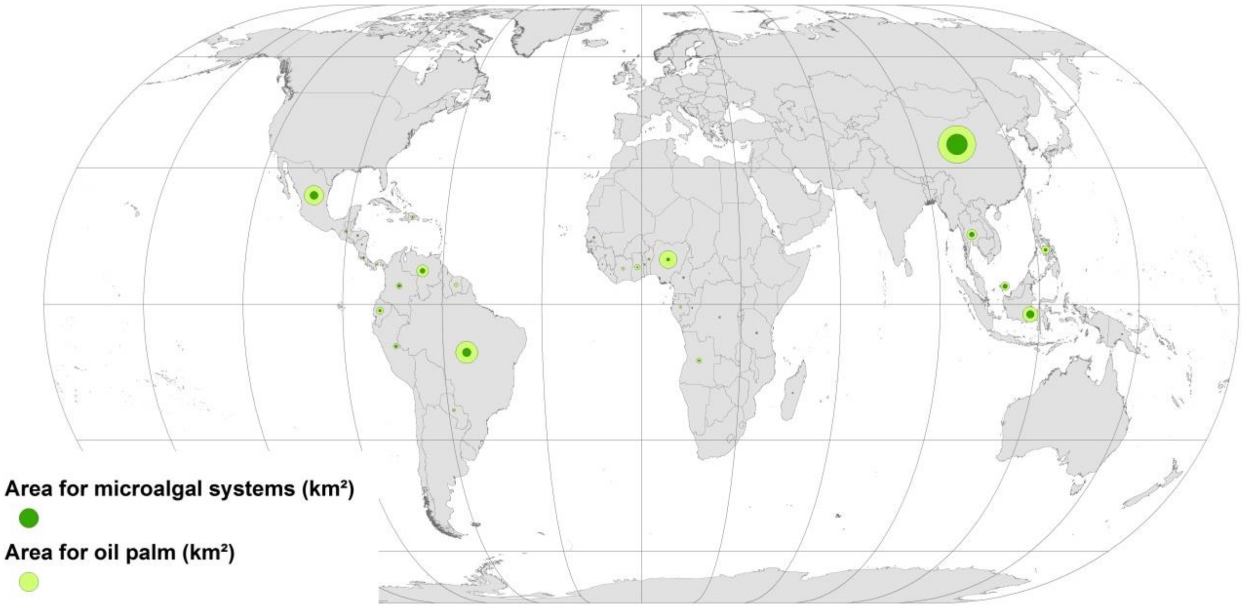

Figure S2. Superimposed circles showing the cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, when comparing microalgae with oil palm production.

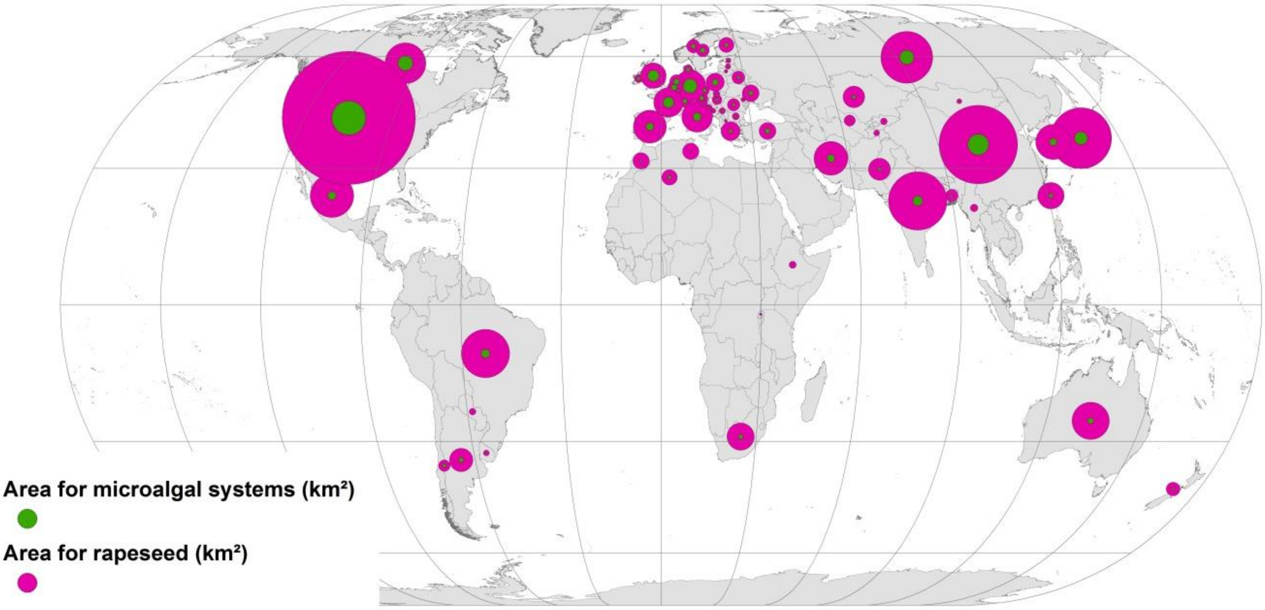

Figure S3. Superimposed circles showing the cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, when comparing microalgae with rapeseed production.

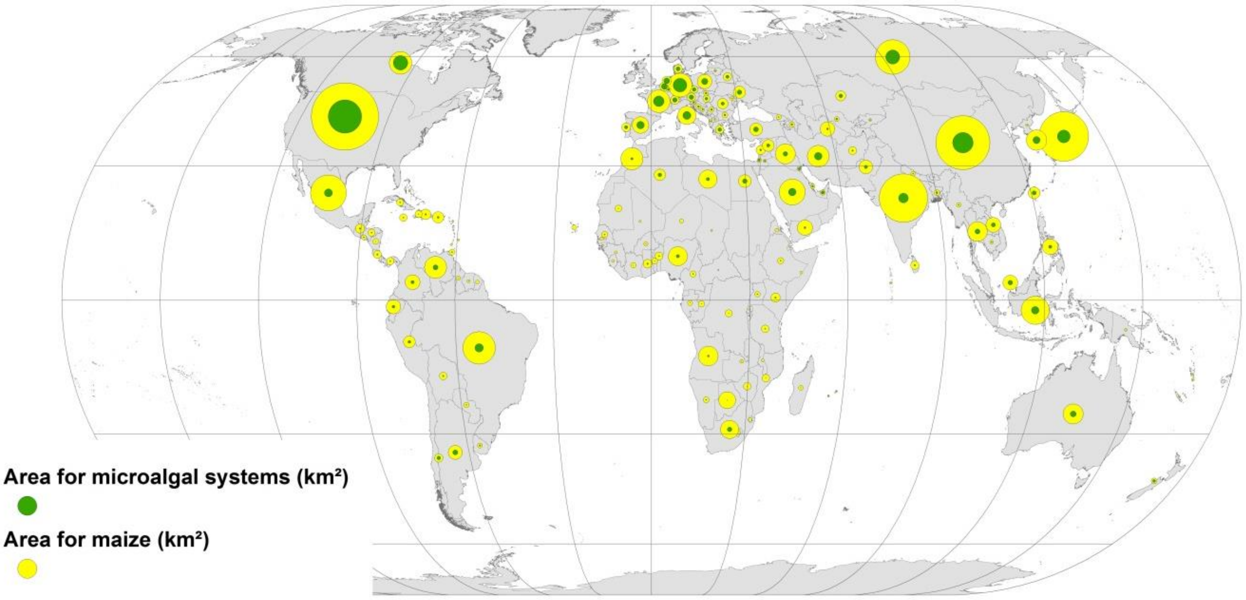

Figure S4. Superimposed circles showing the cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, when comparing microalgae with maize production.

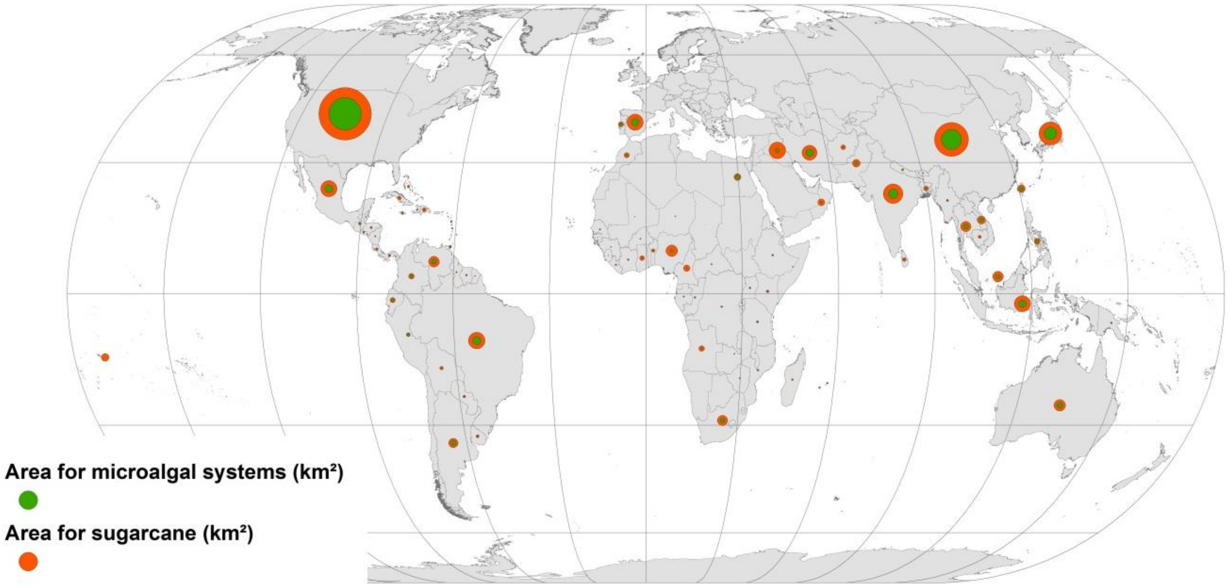

Figure S5. Superimposed circles showing the cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, when comparing microalgae with sugarcane production.

Table S7. Cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010 when comparing microalgae with soybean production. Relative cultivation area of microalgal systems in comparison to soybean is showed.

Country	Area (km^2) for soybean	Area (km^2) for microalgae	Relative cultivation area of microalgal systems (%)
Albania	32,074.9	811.9	2.5
Angola	534,072.4	2,663.3	0.5
Argentina	460,958.9	16,235.9	3.5
Australia	1,030,702.7	22,653.9	2.2
Austria	250,978.1	13,493.5	5.4
Azerbaijan	257,566.0	2,166.2	0.8

Bangladesh	128,040.7	2,362.8	1.8
Belize	4,600.8	87.8	1.9
Benin	93,332.9	810.7	0.9
Bhutan	4,886.6	78.2	1.6
Bolivia	70,403.7	1,476.8	2.1
Bosnia and Herzegovina	41,961.3	1,349.7	3.2
Brazil	1,522,318.6	45,995.8	3.0
Bulgaria	112,045.7	2,801.9	2.5
Burkina Faso	22,384.2	321.8	1.4
Burundi	4,623.2	36.5	0.8
Cambodia	33,350.6	625.1	1.9
Cameroon	73,771.8	789.7	1.1
Canada	1,562,018.1	136,433.0	8.7
China	8,927,261.8	276,923.3	3.1
Colombia	255,161.8	6,289.9	2.5
Côte d'Ivoire	53,286.4	597.0	1.1
Croatia	67,656.5	2,977.8	4.4
Czech Republic	202,409.8	9,109.8	4.5
Democratic Republic of the Congo	73,318.6	372.0	0.5
East Timor	3,561.9	44.9	1.3
Ecuador	302,855.7	5,391.9	1.8
Egypt	372,113.3	12,605.4	3.4
El Salvador	35,745.6	779.4	2.2
Ethiopia	68,299.3	896.2	1.3
France	1,455,797.7	74,430.1	5.1
Gabon	47,336.0	396.5	0.8
Georgia	17,099.4	889.6	5.2
Germany	3,460,447.3	117,604.2	3.4
Greece	309,114.3	9,726.2	3.1
Guatemala	60,119.1	1,680.8	2.8
Honduras	36,076.4	870.2	2.4
Hungary	141,792.5	5,982.1	4.2
India	4,633,344.4	59,125.7	1.3
Indonesia	2,366,365.1	36,416.5	1.5
Iran	1,360,744.5	38,078.9	2.8
Iraq	939,856.3	12,945.3	1.4
Italy	852,517.8	44,140.6	5.2
Japan	3,618,903.5	108,241.5	3.0
Kazakhstan	245,002.4	8,466.4	3.5
Kenya	125,386.3	1,340.8	1.1
Kyrgyzstan	47,875.9	854.6	1.8
Laos	2,615.1	47.7	1.8
Liberia	17,676.3	82.4	0.5
Macedonia	19,057.2	569.9	3.0
Madagascar	55,797.8	313.5	0.6
Malawi	17,194.6	162.3	0.9
Mali	12,717.9	126.2	1.0
Mexico	2,386,561.3	42,614.4	1.8
Moldova	29,498.4	819.8	2.8
Morocco	361,105.7	4,152.2	1.1
Myanmar	55,889.7	884.7	1.6
Nepal	49,177.1	636.7	1.3
Nicaragua	20,951.6	469.0	2.2
Nigeria	675,080.2	6,716.3	1.0
North Korea	25,735.5	580.0	2.3
Pakistan	908,321.9	7,632.0	0.8
Panama	271,236.6	1,045.4	0.4
Paraguay	38,026.0	1,001.0	2.6
Peru	238,169.0	4,730.6	2.0

Philippines	373,222.8	7,560.3	2.0
Poland	830,458.6	26,993.4	3.3
Romania	200,392.8	7,130.0	3.6
Russia	3,721,409.7	125,951.9	3.4
Rwanda	13,707.9	99.4	0.7
Serbia	53,867.3	2,383.4	4.4
Slovakia	86,694.1	3,155.2	3.6
Slovenia	66,053.2	3,071.3	4.6
South Africa	755,214.2	14,494.9	1.9
South Korea	1,144,272.0	35,056.7	3.1
Spain	1,050,103.2	38,059.4	3.6
Sri Lanka	103,285.9	1,877.9	1.8
Suriname	26,335.2	302.5	1.1
Switzerland	260,834.8	14,023.0	5.4
Syria	280,799.2	6,401.4	2.3
Taiwan	442,550.0	12,032.8	2.7
Tajikistan	92,929.4	297.1	0.3
Tanzania	82,445.1	737.6	0.9
Thailand	479,291.9	17,837.0	3.7
Togo	87,664.6	417.6	0.5
Turkey	311,855.3	16,833.9	5.4
Uganda	63,672.4	629.9	1.0
Ukraine	427,075.8	13,791.7	3.2
United States	14,210,193.3	716,924.0	5.0
Uruguay	48,348.8	1,296.3	2.7
Venezuela	1,111,923.4	17,659.3	1.6
Vietnam	581,580.5	10,683.5	1.8
Zambia	17,114.3	324.2	1.9
Zimbabwe	27,018.8	409.0	1.5

Table S8. Cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, for oil palm in comparison to microalgal systems. Relative cultivation area of microalgal systems in comparison to oil palm is showed.

Country	Area (km^2) for oil palm	Area (km^2) for microalgae	Relative cultivation area of microalgal systems (%)
Angola	17,795.7	2,663.3	15.0
Benin	3,914.9	810.7	20.7
Brazil	309,386.5	45,995.8	14.9
Burundi	294.5	36.5	12.4
Cameroon	3,084.0	789.7	25.6
Central African Republic	332.4	33.6	10.1
China	897,755.2	276,923.3	30.8
Colombia	23,322.3	6,289.9	27.0
Costa Rica	5,996.7	1,287.4	21.5
Côte d'Ivoire	6,791.0	597.0	8.8
Democratic Republic of the Congo	4,487.2	372.0	8.3
Dominican Republic	8,444.6	1,647.7	19.5
Ecuador	31,608.4	5,391.9	17.1
Equatorial Guinea	954.2	128.7	13.5
Gabon	4,903.4	396.5	8.1
Gambia	753.3	98.2	13.0
Ghana	17,907.6	1,329.7	7.4
Guatemala	6,541.5	1,680.8	25.7
Guinea	3,627.6	130.0	3.6
Guinea-Bissau	389.5	43.0	11.0
Honduras	4,126.3	870.2	21.1
Indonesia	149,733.7	36,416.5	24.3
Liberia	584.8	82.4	14.1
Madagascar	2,019.6	313.5	15.5

Malaysia	48,182.3	14,884.0	30.9
Mexico	238,950.8	42,614.4	17.8
Nicaragua	1,669.2	469.0	28.1
Nigeria	194,867.7	6,716.3	3.4
Panama	7,746.8	1,045.4	13.5
Papua New Guinea	1,931.1	377.1	19.5
Paraguay	7,547.2	1,001.0	13.3
Peru	20,838.1	4,730.6	22.7
Philippines	45,276.0	7,560.3	16.7
Republic of Congo	2,135.3	348.9	16.3
Sao Tome and Principe	169.0	22.1	13.1
Senegal	4,400.9	611.1	13.9
Sierra Leone	1,103.5	117.5	10.6
Solomon Islands	216.8	47.3	21.8
Suriname	11,156.2	302.5	2.7
Tanzania	4,126.9	737.6	17.9
Thailand	67,481.7	17,837.0	26.4
Togo	3,609.3	417.6	11.6
Venezuela	94,294.4	17,659.3	18.7

Table S9. Cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, for rapeseed in comparison to microalgal systems. Relative cultivation area of microalgal systems in comparison to rapeseed is showed.

Country	Area (km^2) for rapeseed	Area (km^2) for microalgae	Relative cultivation area of microalgal systems (%)
Algeria	150,194.3	8,747.7	5.8
Argentina	346,673.5	16,235.9	4.7
Australia	875,244.0	22,653.9	2.6
Austria	98,358.3	13,493.5	13.7
Bangladesh	97,810.4	2,362.8	2.4
Belarus	102,608.2	7,066.9	6.9
Belgium	108,949.2	21,891.3	20.1
Bosnia and Herzegovina	17,236.8	1,349.7	7.8
Brazil	1,472,945.2	45,995.8	3.1
Bulgaria	34,895.3	2,801.9	8.0
Canada	1,059,209.8	136,433.0	12.9
Chile	87,281.6	10,181.4	11.7
China	3,846,822.5	276,923.3	7.2
Croatia	29,681.1	2,977.8	10.0
Czech Republic	62,947.6	9,109.8	14.5
Denmark	52,328.8	10,328.2	19.7
Estonia	17,298.1	1,488.5	8.6
Ethiopia	31,920.1	896.2	2.8
Finland	142,407.0	11,557.3	8.1
France	547,623.3	74,430.1	13.6
Germany	632,743.3	117,604.2	18.6
Greece	223,398.6	9,726.2	4.4
Hungary	59,186.1	5,982.1	10.1
India	2,137,788.5	59,125.7	2.8
Iran	725,049.9	38,078.9	5.3
Ireland	42,900.0	8,813.8	20.5
Italy	601,534.6	44,140.6	7.3
Japan	2,317,352.6	108,241.5	4.7
Kazakhstan	294,975.2	8,466.4	2.9
Kyrgyzstan	28,780.0	854.6	3.0
Latvia	19,678.9	2,029.7	10.3
Lithuania	8,651.4	824.3	9.5
Luxembourg	22,559.3	3,666.1	16.3
Macedonia	7,424.9	569.9	7.7

Mexico	1,196,178.5	42,614.4	3.6
Moldova	14,704.5	819.8	5.6
Mongolia	15,708.1	1,187.6	7.6
Morocco	166,473.5	4,152.2	2.5
Myanmar	38,066.8	884.7	2.3
Netherlands	118,787.2	22,275.5	18.8
New Zealand	122,777.3	5,583.8	4.5
Norway	112,313.7	12,947.3	11.5
Pakistan	309,354.2	7,632.0	2.5
Paraguay	150,194.3	8,747.7	3.5
Poland	346,673.5	16,235.9	13.1
Romania	875,244.0	22,653.9	7.1
Russia	98,358.3	13,493.5	7.4
Rwanda	97,810.4	2,362.8	1.6
Serbia	102,608.2	7,066.9	9.5
Slovakia	108,949.2	21,891.3	10.4
Slovenia	17,236.8	1,349.7	10.8
South Africa	1,472,945.2	45,995.8	3.1
South Korea	34,895.3	2,801.9	4.5
Spain	1,059,209.8	136,433.0	5.6
Sweden	87,281.6	10,181.4	16.1
Switzerland	3,846,822.5	276,923.3	13.9
Taiwan	29,681.1	2,977.8	2.7
Tajikistan	62,947.6	9,109.8	1.3
Tunisia	52,328.8	10,328.2	1.1
Turkey	17,298.1	1,488.5	9.4
Ukraine	31,920.1	896.2	7.9
United Kingdom	142,407.0	11,557.3	18.8
United States	547,623.3	74,430.1	6.5
Uruguay	632,743.3	117,604.2	5.7
Uzbekistan	223,398.6	9,726.2	3.2

Table S10. Cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, for maize in comparison to microalgal systems. Relative cultivation area of microalgal systems in comparison to maize is showed.

Country	Area (km^2) for maize	Area (km^2) for microalgae	Relative cultivation area of microalgal systems (%)
Afghanistan	42,210.7	1,650.1	3.9
Albania	6,425.7	811.9	12.6
Algeria	83,486.8	8,747.7	10.5
Angola	247,988.1	2,663.3	1.1
Antigua and Barbuda	2,654.8	74.8	2.8
Argentina	124,018.6	16,235.9	13.1
Armenia	2,890.5	351.4	12.2
Australia	255,091.2	22,653.9	8.9
Austria	44,694.1	13,493.5	30.2
Azerbaijan	20,156.8	2,166.2	10.7
Bahamas	4,104.0	377.5	9.2
Bangladesh	22,623.0	2,362.8	10.4
Barbados	3,545.9	153.1	4.3
Belarus	45,464.6	7,066.9	15.5
Belgium	58,310.4	21,891.3	37.5
Belize	1,979.9	87.8	4.4
Benin	41,714.7	810.7	1.9
Bhutan	1,471.2	78.2	5.3
Bolivia	35,770.3	1,476.8	4.1
Bosnia and Herzegovina	12,475.7	1,349.7	10.8
Botswana	184,129.1	590.2	0.3
Brazil	680,227.0	45,995.8	6.8

Bulgaria	23,365.7	2,801.9	12.0
Burkina Faso	12,300.9	321.8	2.6
Burundi	2,264.0	36.5	1.6
Cambodia	9,151.8	625.1	6.8
Cameroon	25,323.2	789.7	3.1
Canada	328,354.5	136,433.0	41.6
Cape Verde	16,916.5	48.8	0.3
Central African Republic	1,746.3	33.6	1.9
Chad	2,427.9	39.5	1.6
Chile	44,580.3	10,181.4	22.8
China	1,875,195.6	276,923.3	14.8
Colombia	140,179.8	6,289.9	4.5
Comoros	583.3	22.5	3.9
Costa Rica	40,598.9	1,287.4	3.2
Côte d'Ivoire	18,384.1	597.0	3.2
Croatia	17,739.1	2,977.8	16.8
Cuba	33,795.7	1,175.0	3.5
Czech Republic	38,239.2	9,109.8	23.8
Democratic Republic of the Congo	32,090.4	372.0	1.2
Denmark	48,422.6	10,328.2	21.3
Djibouti	2,317.2	57.6	2.5
Dominica	42,210.7	1,650.1	2.2
Dominican Republic	6,425.7	811.9	2.3
East Timor	83,486.8	8,747.7	2.8
Ecuador	247,988.1	2,663.3	4.1
Egypt	2,654.8	74.8	12.1
El Salvador	124,018.6	16,235.9	4.6
Eritrea	2,890.5	351.4	1.2
Ethiopia	255,091.2	22,653.9	3.7
Fiji	44,694.1	13,493.5	3.1
France	20,156.8	2,166.2	22.5
French Guiana	4,104.0	377.5	1.5
Gabon	22,623.0	2,362.8	2.6
Gambia	3,545.9	153.1	1.6
Georgia	45,464.6	7,066.9	5.4
Germany	58,310.4	21,891.3	31.6
Ghana	1,979.9	87.8	2.7
Greece	41,714.7	810.7	21.1
Grenada	1,471.2	78.2	1.5
Guam	35,770.3	1,476.8	4.2
Guatemala	12,475.7	1,349.7	3.1
Guinea	184,129.1	590.2	2.1
Guinea-Bissau	680,227.0	45,995.8	1.7
Guyana	23,365.7	2,801.9	2.2
Haiti	12,300.9	321.8	1.2
Honduras	2,264.0	36.5	2.5
Hungary	9,151.8	625.1	17.3
India	25,323.2	789.7	3.9
Indonesia	328,354.5	136,433.0	7.0
Iran	16,916.5	48.8	12.5
Iraq	1,746.3	33.6	4.9
Israel	2,427.9	39.5	38.7
Italy	44,580.3	10,181.4	20.7
Jamaica	1,875,195.6	276,923.3	1.9
Japan	140,179.8	6,289.9	6.7
Jordan	583.3	22.5	30.5
Kazakhstan	40,598.9	1,287.4	13.0
Kenya	18,384.1	597.0	2.3
Kuwait	17,739.1	2,977.8	50.1

Kyrgyzstan	33,795.7	1,175.0	14.1
Laos	38,239.2	9,109.8	9.2
Lebanon	32,090.4	372.0	5.7
Lesotho	48,422.6	10,328.2	1.0
Libya	2,317.2	57.6	3.4
Lithuania	42,210.7	1,650.1	17.3
Luxembourg	6,425.7	811.9	24.7
Macedonia	83,486.8	8,747.7	9.7
Madagascar	247,988.1	2,663.3	2.3
Malawi	2,654.8	74.8	3.0
Malaysia	124,018.6	16,235.9	10.2
Maldives	2,890.5	351.4	6.1
Mali	255,091.2	22,653.9	3.5
Mauritania	44,694.1	13,493.5	1.1
Mauritius	20,156.8	2,166.2	11.9
Mexico	4,104.0	377.5	5.0
Moldova	22,623.0	2,362.8	7.6
Montenegro	3,545.9	153.1	9.1
Montserrat	45,464.6	7,066.9	9.2
Morocco	58,310.4	21,891.3	1.3
Mozambique	1,979.9	87.8	1.4
Myanmar	41,714.7	810.7	6.3
Namibia	1,471.2	78.2	3.0
Nepal	35,770.3	1,476.8	4.3
Netherlands	12,475.7	1,349.7	41.2
New Caledonia	184,129.1	590.2	5.9
New Zealand	680,227.0	45,995.8	26.1
Nicaragua	23,365.7	2,801.9	2.2
Niger	12,300.9	321.8	1.3
Nigeria	2,264.0	36.5	2.8
North Korea	9,151.8	625.1	10.0
Pakistan	25,323.2	789.7	6.3
Panama	328,354.5	136,433.0	2.8
Papua New Guinea	16,916.5	48.8	8.0
Paraguay	1,746.3	33.6	5.1
Peru	2,427.9	39.5	5.1
Philippines	44,580.3	10,181.4	4.6
Poland	1,875,195.6	276,923.3	20.1
Portugal	140,179.8	6,289.9	13.6
Puerto Rico	583.3	22.5	2.7
Qatar	40,598.9	1,287.4	23.2
Republic of Congo	18,384.1	597.0	1.4
Reunion	17,739.1	2,977.8	13.2
Romania	33,795.7	1,175.0	9.5
Russia	38,239.2	9,109.8	16.1
Rwanda	32,090.4	372.0	2.4
Saint Vincent and the Grenadines	48,422.6	10,328.2	29.3
Sao Tome and Principe	2,317.2	57.6	2.4
Saudi Arabia	42,210.7	1,650.1	8.2
Senegal	6,425.7	811.9	2.4
Serbia	83,486.8	8,747.7	13.0
Sierra Leone	247,988.1	2,663.3	2.2
Slovakia	2,654.8	74.8	18.5
Slovenia	124,018.6	16,235.9	21.0
Somalia	2,890.5	351.4	1.9
South Africa	255,091.2	22,653.9	6.7
South Korea	44,694.1	13,493.5	12.8
Spain	20,156.8	2,166.2	21.2
Sri Lanka	4,104.0	377.5	4.0

Suriname	22,623.0	2,362.8	3.9
Swaziland	3,545.9	153.1	1.9
Switzerland	45,464.6	7,066.9	26.7
Syria	58,310.4	21,891.3	6.9
Taiwan	1,979.9	87.8	12.9
Tajikistan	41,714.7	810.7	20.1
Tanzania	1,471.2	78.2	2.0
Thailand	35,770.3	1,476.8	7.3
Togo	12,475.7	1,349.7	1.8
Trinidad and Tobago	184,129.1	590.2	3.8
Turkey	680,227.0	45,995.8	15.6
Turkmenistan	23,365.7	2,801.9	2.2
Uganda	12,300.9	321.8	3.2
Ukraine	2,264.0	36.5	14.1
United Arab Emirates	9,151.8	625.1	39.3
United States	25,323.2	789.7	24.3
Uruguay	328,354.5	136,433.0	8.2
Uzbekistan	16,916.5	48.8	16.9
Vanuatu	1,746.3	33.6	0.9
Venezuela	2,427.9	39.5	5.6
Vietnam	44,580.3	10,181.4	7.4
Yemen	1,875,195.6	276,923.3	2.2
Zambia	140,179.8	6,289.9	3.5
Zimbabwe	583.3	22.5	1.1

Table S11. Cultivation area (km^2) required to meet gasoline and distillate fuel oil demands for each country in 2010, for sugarcane in comparison to microalgal systems. Relative cultivation area of microalgal systems in comparison to sugarcane is showed.

Country	Area (km^2) for sugarcane	Area (km^2) for microalgae	Relative cultivation area of microalgal systems (%)
Afghanistan	17,785.5	1,650.1	9.3
American Samoa	40,626.1	126.2	0.3
Angola	23,656.6	2,663.3	11.3
Argentina	60,132.9	16,235.9	27.0
Australia	91,133.2	22,653.9	24.9
Bahamas	4,850.1	377.5	7.8
Bangladesh	17,211.9	2,362.8	13.7
Barbados	1,131.8	153.1	13.5
Belize	653.1	87.8	13.4
Benin	9,429.8	810.7	8.6
Bhutan	613.1	78.2	12.8
Bolivia	9,319.9	1,476.8	15.8
Brazil	188,711.3	45,995.8	24.4
Burkina Faso	1,017.9	321.8	31.6
Burundi	193.4	36.5	18.9
Cambodia	7,909.1	625.1	7.9
Cameroon	27,761.7	789.7	2.8
Cape Verde	749.4	48.8	6.5
Central African Republic	1,555.3	33.6	2.2
Chad	133.4	39.5	29.6
China	769,456.6	276,923.3	36.0
Colombia	21,516.6	6,289.9	29.2
Costa Rica	5,530.9	1,287.4	23.3
Côte d'Ivoire	2,612.7	597.0	22.9
Cuba	11,044.1	1,175.0	10.6
Democratic Republic of the Congo	2,939.7	372.0	12.7
Dominica	475.6	28.5	6.0
Dominican Republic	10,512.5	1,647.7	15.7
Ecuador	20,468.2	5,391.9	26.3

Egypt	35,047.3	12,605.4	36.0
El Salvador	3,017.8	779.4	25.8
Ethiopia	2,772.5	896.2	32.3
Fiji	1,328.6	190.8	14.4
French Guiana	668.5	129.4	19.4
French Polynesia	621.4	148.4	23.9
Gabon	2,149.2	396.5	18.4
Ghana	16,492.4	1,329.7	8.1
Grenada	389.6	53.7	13.8
Guadeloupe	1,609.6	295.8	18.4
Guatemala	5,848.9	1,680.8	28.7
Guinea	773.3	130.0	16.8
Guinea-Bissau	516.9	43.0	8.3
Guyana	1,361.0	268.0	19.7
Haiti	17,785.5	1,650.1	19.5
Honduras	40,626.1	126.2	25.2
India	23,656.6	2,663.3	22.4
Indonesia	60,132.9	16,235.9	20.5
Iran	91,133.2	22,653.9	25.1
Iraq	4,850.1	377.5	6.8
Jamaica	17,211.9	2,362.8	16.6
Japan	1,131.8	153.1	30.5
Kenya	653.1	87.8	23.7
Laos	9,429.8	810.7	16.3
Liberia	613.1	78.2	3.3
Madagascar	9,319.9	1,476.8	9.9
Malawi	188,711.3	45,995.8	32.5
Malaysia	1,017.9	321.8	19.0
Mali	193.4	36.5	22.8
Martinique	7,909.1	625.1	15.6
Mauritius	27,761.7	789.7	22.4
Mexico	749.4	48.8	23.3
Morocco	1,555.3	33.6	20.7
Mozambique	133.4	39.5	21.1
Myanmar	769,456.6	276,923.3	21.7
Nepal	21,516.6	6,289.9	16.4
Nicaragua	5,530.9	1,287.4	27.8
Niger	2,612.7	597.0	15.5
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Oman	2,939.7	372.0	7.0
Pakistan	475.6	28.5	18.3
Panama	10,512.5	1,647.7	19.0
Papua New Guinea	20,468.2	5,391.9	12.8
Paraguay	35,047.3	12,605.4	16.2
Peru	3,017.8	779.4	42.1
Philippines	2,772.5	896.2	27.5
Portugal	1,328.6	190.8	33.8
Republic of Congo	668.5	129.4	11.7
Reunion	621.4	148.4	22.9
Rwanda	2,149.2	396.5	7.7
Saint Kitts and Nevis	16,492.4	1,329.7	16.6
Saint Vincent and the Grenadines	389.6	53.7	7.6
Samoa	1,609.6	295.8	3.9
Senegal	5,848.9	1,680.8	35.3
Sierra Leone	773.3	130.0	22.0
Somalia	516.9	43.0	9.8
South Africa	1,361.0	268.0	19.8
Spain	17,785.5	1,650.1	21.1
Sri Lanka	40,626.1	126.2	17.9

Suriname	23,656.6	2,663.3	12.6
Swaziland	60,132.9	16,235.9	31.1
Taiwan	91,133.2	22,653.9	28.5
Tanzania	4,850.1	377.5	20.4
Thailand	17,211.9	2,362.8	24.0
Trinidad and Tobago	1,131.8	153.1	16.6
Uganda	653.1	87.8	19.7
United States	9,429.8	810.7	38.6
Uruguay	613.1	78.2	19.3
Venezuela	9,319.9	1,476.8	22.5
Vietnam	188,711.3	45,995.8	22.4
Zambia	1,017.9	321.8	30.8
Zimbabwe	193.4	36.5	23.1

3. Calculation of water footprint for microalgal production systems

Table S12 shows the amount of green and blue water consumed per unit of produced green diesel (wet conversion), assuming water recycling, following the calculations from Gerbens-Leenes et al. (2014) for open ponds and photobioreactors in several locations: New Mexico, Perth, Hawaii, Italy, The Netherlands, France and Algeria.

Table S12. Green and blue water footprint per energy unit of produced green biodiesel.Based on calculations by Gerbens-Leenes et al. (2014) for obtaining of microalgal biodiesel through wet conversion, assuming water recycling. Photobioreactor (PB).

Locations	Microalgal system	Length growing period (days)	Cultivation Area (m^2)	Area covered with ponds (m^2)	Annual dry biomass production (tonnes year^{-1})	Total green diesel energy production (GJ)	Daily mean evaporation (mm day^{-1})	Annual pond evaporation (kL)	Annual evaporative cooling (kL ha^{-1})	Green and blue water footprint (kL GJ^{-1})
New Mexico	Open pond (salt water)	365.0	2,000.0	2,150.0	7.3	95.2	2.3	1,781.0	-	18.7
Perth	Open pond (salt water)	300.0	1.0	1.1	0.0	0.1	2.8	0.9	-	12.6
Hawaii	Open pond/PB (fresh water)	365.0	601.0	417.0	2.3	18.6	4.0	606.0	-	32.6
Italy	PB	180.0	10,000.0	-	32.0	521.7	-	-	4,485.0	8.6
The Netherlands	PB	365.0	10,000.0	-	115.0	749.9	-	-	2,030.0	2.7
France	PB	365.0	10,000.0	-	155.0	1,010.7	-	-	9,530.0	9.4
Algeria	PB	365.0	10,000.0	-	185.0	1,202.6	-	-	27,752.0	23.1

Chapter 2. Contribution to the authorship

I was in charge of the conception and design of the project; acquisition, analysis, and interpretation of the research data; drafting, analysis, and critical writing of the manuscript; and sending of the manuscript to peer-reviewed journals (i.e., as corresponding author).

CHAPTER 2. Global mapping of cost-effective microalgal biofuel production areas with minimal environmental impact

Diego F. Correa[1,2*], Hawthorne L. Beyer[2], Hugh P. Possingham[2,3], Skye R. Thomas-Hall[1], Peer M. Schenk[1]

[1]Algae Biotechnology Laboratory, School of Agriculture and Food Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia

[2] Centre for Biodiversity and Conservation Science CBCS, The University of Queensland, Brisbane, Queensland 4072, Australia

[3]The Nature Conservancy, Arlington, VA 22203, USA

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ABSTRACT

Sustainable alternatives to fossil fuels are urgently needed to avoid severe climate impacts and further environmental degradation. Microalgae are one of the most productive crops globally and do not need to compete for arable land or freshwater resources. Hence, they may become a promising, more sustainable cultivation alternative for the large-scale production of biofuels provided substantial reductions are achieved in their production costs. In this study, we identify the most suitable areas globally for siting microalgal farms for biodiesel production that maximize profitability and minimize direct competition with food production and direct impacts on biodiversity, based on a spatially explicit multiple-criteria decision analysis (MCDA). We further explore the relationships between microalgal production, agricultural value, and biodiversity, and propose several solutions for siting microalgal production farms, based on current and future targets in energy production using integer linear programming. If using seawater for microalgal cultivation, biodiesel production could reach 4.17×10^{11} L year^{-1} based on top suitable lands (i.e., between 10% and 12% of total transport energy demands in 2030) without directly competing with food production and areas of high biodiversity value. These areas are particularly abundant in the dry coasts of North and East Africa, the Middle East, and western South America. This is the first global analysis that incorporates economic and environmental feasibility for microalgal production sites. Our results can guide the selection of best locations for biofuel production using microalgae while minimizing conflicts with food production and biodiversity conservation.

Keywords: Biodiversity, biofuel, fossil fuel, energy, food, GIS, microalgae, renewable, sustainability

1. INTRODUCTION

Rapid climate change is having profound impacts on social and environmental systems globally, and these threats are expected to become substantially more severe in the coming decades (MEA 2005, Scheffers et al. 2016). In 2016, the energy sector emitted around 32 Gt CO_2 into the atmosphere, mostly from fossil fuel use (IEA 2017). The replacement of fossil fuels is an urgent component of efforts to prevent global warming from exceeding 2°C compared to pre-industrial levels, a commitment that has been ratified by 185 parties following the 21st Conference of the Parties (COP) to the United Nations Framework Convention on Climate Change (UNFCCC) (IPCC 2015). Through the transformation of biomass into bioenergy (McKendry 2002), biofuel systems can provide an alternative to fossil fuels in the transport sector, especially for the shipping and aviation industries, which in the mid-term cannot be fully powered by electricity (Fulton et al. 2015).

However, first generation biofuels, which derive from food crops (e.g., maize, sugarcane, soybean, and oil palm), compete with food production (Pimentel et al. 2009, Tilman et al. 2009) and drive environmental degradation (Fargione et al. 2008, Searchinger et al. 2008, Fargione et al. 2010, Immerzeel et al. 2014, Correa et al. 2017), directly competing for agricultural lands and leading to habitat loss for native species (Koh 2007, Fargione et al. 2010, Koh et al. 2011, Immerzeel et al. 2014, Correa et al. 2017). Furthermore, they have been linked to increases in CO_2 emissions after carbon-rich systems (e.g., forests and native grasslands) are transformed into biofuel monocultures, which can negate their potential for climate change mitigation (Fargione et al. 2008, Searchinger et al. 2008, Searchinger et al. 2015). At a projected population of 9 billion people and a 60% increase in food demand by 2050 compared to 2006 (FAO 2016), biofuel systems not only need to offer climate change mitigation (IPCC 2015) but also must have limited competition with food production and biodiverse lands (CBD 2011, Foley et al. 2011). These goals could be achieved by increasing the productivity of first generation biofuels and their co-products (e.g., food and animal feed) within current production areas (Souza et al. 2015, Tomei and Helliwell 2016, IEA 2017) while preventing their expansion into agricultural lands and biodiverse regions (Foley et al. 2011, Souza et al. 2015), coupled with the adoption of systems that do not rely on arable lands (e.g., wastes and microalgae)

(Tilman et al. 2009, Correa et al. 2017) able to gradually replace less sustainable biofuel production alternatives (Correa et al. 2019). Microalgal biofuel production systems (i.e., third generation biofuels) are based on the cultivation of prokaryotic and eukaryotic photosynthetic microorganisms (i.e., microalgae) in recirculation channels open to the atmosphere (i.e., open ponds) or in enclosed culture devices (i.e., photobioreactors), making use of water (fresh, brackish or salt water) and nutrients (Chisti 2007, Schenk et al. 2008, Lundquist et al. 2010, Mata et al. 2010). The lipids and carbohydrates contained in microalgal cells can be respectively converted into biodiesel and bioethanol, helping to offset liquid fossil fuels (i.e., diesel and gasoline) (Schenk et al. 2008, Mata et al. 2010) as well as produce biohydrogen or biogas (Schenk et al. 2008). These systems are a promising alternative for future biofuel production (Aro 2016), primarily because they need less land for producing the same amount of energy compared to first generation biofuels, and additionally because they do not need fertile soils for their cultivation (Chisti 2007, Schenk et al. 2008, Mata et al. 2010, Quinn and Davis 2015, Correa et al. 2017). These advantages could decrease direct competition with agricultural and biodiverse lands, leading to lower competition with food production and reduced habitat loss for native species (Correa et al. 2017), or free lands for further agricultural production, ecological restoration, and biodiversity conservation (Walsh et al. 2015). While technological advances in the cultivation, harvesting, and conversion of microalgae into biofuels increase the cost-effectiveness and sustainability of microalgal production systems (Yang et al. 2011, Mu et al. 2014, Uggetti et al. 2014, Venteris et al. 2014, González-González et al. 2018), further steps are needed to identify the most profitable areas for microalgal biofuel production without competing for arable lands or biodiverse landscapes.

With 16% of transport energy demands potentially fulfilled by biofuels in 2040 (IEA 2017), microalgal biofuel production systems could become an important alternative for offsetting fossil fuels in the transport sector, provided that significant reductions in their production costs are achieved (Norsker et al. 2011, Slade and Bauen 2013, Acién et al. 2018, Chia et al. 2018). Costs reductions can derive from the development of biorefinery systems that produce high-value co-products (e.g., food and animal feed) along with biofuels (Ruiz et al. 2016, Chia et al. 2018); the identification, development, and cultivation of fast-growing microalgal strains (Mata et al. 2010, Ajjawi et al. 2017); the co-location of microalgal production systems with free nutrient and CO_2 sources (e.g., from wastewater operations and industries) (Mu et al. 2014, Orfield et al. 2014, Roostaei and Zhang 2017, Beal et al. 2018); the production of biogas and the recycling of nutrients (i.e., by anaerobic digestion) (Uggetti et al. 2014, González-González et al. 2018); and the implementation of governmental incentives based on the relative environmental benefits of biofuel production alternatives (Correa et al. 2019). However, considerable land areas will still be required to offset fossil fuels by microalgal cultivation, although lower compared to first generation biofuels (Chisti 2008, Correa et al. 2017). Here, we evaluate global opportunities for large-scale microalgal biodiesel production while minimizing direct competition with agricultural lands and biodiverse areas, taking into account attributes that maximize the profitability in microalgal biodiesel production: water availability, lipid productivity, flat land availability, proximity to main transport networks, gross national income (GNI) per capita (as a substitute for labor costs), and proximity to known industrial CO_2 sources. Based on four scenarios for microalgal cultivation, which combine two main approaches to decrease microalgal production costs and freshwater use (i.e., availability of free CO_2 and availability of seawater)—Scenario 1 (i.e., use of fresh, brackish or salt water), Scenario 2 (i.e., use of fresh, brackish or salt water adjacent to known industrial CO_2 sources), Scenario 3 (i.e., use of seawater), and Scenario 4 (i.e., use of seawater adjacent to known industrial CO_2 sources)—we: 1) Identify the most suitable areas globally for siting microalgal farms for biodiesel production (i.e., microalgal cultivation systems along with the associated infrastructure), while avoiding direct competition with food production and direct impacts on biodiversity, which are considered the two main impacts of first generation biofuels (Immerzeel et al. 2014, Correa et al. 2017), 2) Explore the relationships between microalgal production, agricultural value, and biodiversity, and 3) Explore solutions for siting microalgal production farms based on current and future targets in energy production. Because we aim at finding areas globally for siting microalgal production farms, we assume free trade for microalgal biofuel commercialization in the context of a globalized economy.

2. MATERIALS AND METHODS

2.1 Development of microalgal suitability model

A GIS-based multiple-criteria decision analysis (MCDA) was developed for selecting suitable areas for large-scale microalgal biodiesel production at a pixel resolution of 5 × 5 km, allowing the identification of large areas (i.e., 25 km^2 $pixel^{-1}$) that meet suitable conditions for microalgal production. GIS-based MCDAs have been widely used in natural resource management and land-use planning (Mendoza and Martins 2006) as they allow the solution of complex decision-making problems through the combination of multiple geographic criteria (Malczewski and Rinner 2015). Three main objectives were considered in the analysis: maximization of profitability in microalgal biodiesel production, minimization of direct competition with food production, and minimization of direct impacts on biodiversity (Fig. S1 in Supplementary Information). Based on the reviewed literature (Lundquist et al. 2010, Klise et al. 2011, Wigmosta et al. 2011, Borowitzka et al. 2012, Fortier and Sturm 2012, Quinn et al. 2012, Venteris et al. 2012, Chiu and Wu 2013, Quinn et al. 2013, Venteris et al. 2013, Bennett et al. 2014, Coleman et al. 2014, Orfield et al. 2014, Prasad et al. 2014, Venteris et al. 2014, Venteris et al. 2014, Venteris et al. 2014, Boruff et al. 2015, Bravo-Fritz et al. 2015, Sharma et al. 2015, Mohseni et al. 2016, Niblick and Landis 2016, Roostaei and Zhang 2017), a set of attributes that capture the complexity of microalgal biodiesel production were selected, either because they are essential for microalgal cultivation or because they have shown to maximize the profitability of microalgal biodiesel production (Sharma et al. 2015): water availability, lipid productivity, availability of flat lands, proximity to main transport networks (i.e., main roads and railroads), GNI per capita (used as a substitute for the availability of low labor costs), and proximity to known industrial CO_2 sources. Water availability is essential for microalgal cultivation (Chisti 2007, Schenk et al. 2008) while lipid productivity is proportional to biodiesel production, increasing the profitability of microalgal biofuel production (Quinn et al. 2011, Slade and Bauen 2013, Moody et al. 2014). Water can be obtained from freshwater sources (i.e., water from precipitation, rivers, irrigation dams, or fresh groundwater sources), brackish water sources (e.g., brackish groundwater sources), and salt water sources (i.e., salt groundwater sources or seawater) (Chisti 2007, Schenk et al. 2008, Venteris et al. 2013). The use of flat lands decreases the costs for ground leveling when constructing microalgal ponds, as well as the costs related to water pumping (Darzins et al. 2010, Lundquist et al. 2010, Wigmosta et al. 2011, Borowitzka et al. 2012, Quinn et al. 2012, Venteris et al. 2012). The proximity to main transport networks allows connectivity between production areas, markets, and inputs (e.g., nutrients needed for microalgal cultivation) (Venteris et al. 2014, Venteris et al. 2014, Boruff et al. 2015, Slegers et al. 2015). The availability of low labor costs decreases overall operational costs (Slade and Bauen 2013, Tredici et al. 2016) and the proximity to known industrial CO_2 sources allows the use of free CO_2 that increases biomass production (Lundquist et al. 2010, Klise et al. 2011, Wigmosta et al. 2011, Borowitzka et al. 2012, Quinn et al. 2013, Slade and Bauen 2013, Orfield et al. 2014, Venteris et al. 2014). Although wastewater sources would decrease costs associated with nutrient obtaining, they were not included in the model as they are not consistently mapped globally.

For minimizing competition with food production, the selected attribute corresponded to the agricultural value of lands (i.e., potential annual gross economic rents from agricultural lands) (Naidoo and Iwamura 2007). For minimizing impacts on biodiversity, the selected attribute corresponded to the biodiversity value. Biodiversity value was based on the number of vertebrate species and the number of threatened vertebrate species (i.e., considering amphibians, birds, and mammals) (Jenkins et al. 2013), the presence of islands (which harbor higher proportions of endemic and threatened species compared to the mainland) (Tershy et al. 2015, McCreless et al. 2016), and the presence of areas with low human pressures (which is related to the integrity of ecosystems) based on the Global Human Footprint (Venter et al. 2016). Water bodies (Lehner and Döll 2004), protected areas (UNEP-WCMC 2016), Key Biodiversity Areas (KBA) (BirdLife International 2016), and urban areas (i.e., based on built areas) (Schneider et al. 2009) were assumed to be unsuitable for microalgal cultivation and excluded from final suitability maps (i.e., assigning No Data to water bodies and zero to the other layers).

We developed four scenarios for microalgal cultivation, based on the type of available water and the inclusion of known industrial CO_2 sources (Scenarios 1, 2, 3, and 4): Scenarios 1 and 2 included the use of fresh, brackish or salt water, while Scenarios 3 and 4 included the use of seawater, which is abundant and does not compete with scarce freshwater sources (Vorosmarty et al. 2010, Gleeson et al. 2012). Scenarios 2 and 4 included the proximity to known industrial CO_2 sources (including public electricity and heat production, manufacturing industries and construction, production of minerals, and production of metals, but not to anaerobic digesters as this information is currently not available), which is a cost-effective way to increase microalgal biomass productivities (Lundquist et al. 2010, Klise et al. 2011, Wigmosta et al. 2011, Borowitzka et al. 2012, Quinn et al. 2013, Slade and Bauen 2013, Orfield et al. 2014, Venteris et al. 2014), while Scenarios 1 and 3 did not include the proximity to known industrial CO_2 sources (Figs. S2, S3, S4, S5 in Supplementary Information).

Land covers potentially replaced by microalgal production farms were identified for top suitable microalgal production lands (i.e., suitability values ≥ 0.7), using the MODIS-derived global mosaic for 2012 at a resolution of 5 arcminutes (Channan et al. 2014). The proportion of top suitable lands within politically unstable countries, which could challenge potential large-scale microalgal biofuel production, was calculated based on the Fragile States Index for 2016 (FFP 2017) for Scenarios 2, 3, and 4—which are the most feasible in terms of reduced competition with freshwater—considering countries with total values ≥ 80 as politically unstable. This index is based on social, economic and political risk indicators that lead to higher values in politically unstable countries. Potential biodiesel production was estimated for top suitable lands, along with the percentage of transport energy demands that could be fulfilled based on Scenarios 2, 3 and 4 in 2016, 2030, and 2040 (See Supplementary Information for details). Future transport energy demands were based on the Current Policies, New Policies, and the Sustainable Development Scenarios for 2030 and 2040 (IEA 2017). The Current Policies Scenario takes into account policies that have been enacted in mid-2017 for reducing greenhouse emissions, while the New Policies Scenario additionally includes announced policy intentions for reducing global warming, and the Sustainable Development Scenario aims at limiting global warming consistent with the Paris Agreement and the United Nations 2030 Agenda for Sustainable Development.

2.2 Development of sensitivity analysis on slope and lipid productivities

In order to determine how changes in model parameters influence the siting of microalgal production farms and potential biodiesel production, a sensitivity analysis was developed based on slope and lipid productivities. For this, the slope was increased from a membership midpoint of 5° to 10°, and 15°; and lipid productivity was both increased and decreased in 20% and 40% from a midpoint of 13,000 L ha^{-1} year^{-1} (see Supplementary Information for details on fuzzy memberships and midpoints). We used the one-at-a-time method, in which the changes in values for each factor were evaluated in turn (Malczewski and Rinner 2015).

2.3 Relationships among microalgal production, agricultural value, and biodiversity

The percentage of distribution ranges of threatened vertebrates (i.e., vulnerable, endangered, and critically endangered amphibians, birds, mammals, and reptiles) (BirdLife International and NatureServe 2016, IUCN 2016) overlapping top suitable microalgal production lands (i.e., suitability values ≥ 0.7) was calculated for Scenarios 2, 3, and 4. Potential conflicts among microalgal biodiesel production, agricultural production, and biodiversity were mapped using a color-grading scale for Scenario 1 (i.e., use of fresh, brackish and salt water).

2.4 Siting of microalgal production farms based on targets in transport energy demands

In order to find locations for siting microalgal production farms based on targets in transport energy demands, an integer linear optimization model (Beyer et al. 2016) was developed using the software R and Gurobi Optimizer (see Supplementary Information for calculation details). The model aimed at maximizing profitability while minimizing direct competition with agricultural lands and biodiverse areas through the following formula:

$$\text{maximize} \sum_i P_i^2\, x_i / \left(\text{maximum}(A_i, B_i) + 1\right)$$

subject to

$$\sum_i D_i \, x_i = T$$

$$0 \leq x_i \leq 0.8$$

Where i corresponds to each pixel, P corresponds to microalgal profitability (ranging from 0 to 1), x corresponds to the decision variable given by the software (ranging from 0 to 0.8 and representing the available area for placing microalgal ponds), "maximum" corresponds to the maximum value among agricultural value A (ranging from 0 to 1) and biodiversity value B (ranging from 0 to 1), D corresponds to productivity values in units of energy (GJ pixel^{-1} year^{-1}), and T represents the targets in energy demands globally in 2016, 2030, and 2040 (GJ year^{-1}) based on the IEA (2017) energy production estimates (i.e., Current Policies Scenario, New Policies Scenario and Sustainable Development Scenario). Using the square of the profitability as the numerator and the maximum value between A and B as the denominator, ensures that pixels with low or average profitabilities, and with high agricultural or high biodiversity value, are excluded in the final solutions. Future technological improvements can increase microalgal biofuel productivities per pixel and thus decrease land areas to reach a fixed target in transport energy demands.

We investigated alternative solutions in which the agricultural and biodiversity values were not taken into account (see Supplementary Information), and in which targets in microalgal biodiesel production increased from 10% to 40% based in 2016's transport energy demands. Finally, the amount of cultivation land needed to meet 10%, 20%, 30% and 40% of total transport energy demands in 2016, 2030, and 2040 was determined based in the several IEA (2017) energy production scenarios (Current Policies Scenario, New Policies Scenario, and Sustainable Development Scenario) and current estimated microalgal lipid productivities (Moody et al. 2014).

3. RESULTS

The most suitable areas for microalgal biodiesel production, while avoiding direct competition with agricultural and biodiverse lands, were located in human-transformed dry tropical and subtropical mainlands (Figs. 1, 2). For Scenario 1 (i.e., cultivation based on fresh, brackish or salt water) top suitable microalgal production lands (suitability values ≥ 0.7) could reach around 1,422.8 thousand km^2, concentrated in dry areas in North and East Africa, the Middle East, South and Central Asia, and South America, mainly overlapping with barren and sparsely vegetated lands (60%), open shrublands (22%), and grasslands (9%) (Table 1). Significant competition with scarce freshwater resources would occur in dry areas, where low-density microalgal production farms could be established (Fig. 3). Scenario 2, which is restricted to known industrial CO_2 sources, could reach around 464.2 thousand km^2 mainly over barren and sparsely vegetated lands (57%), open shrublands (17%), and grasslands (8%). The cultivation scenarios 3 and 4 (i.e., cultivation based on seawater) could reach around 305.3 thousand km^2 and 132.9 thousand km^2, respectively, mainly over barren or sparsely vegetated lands and open shrublands.

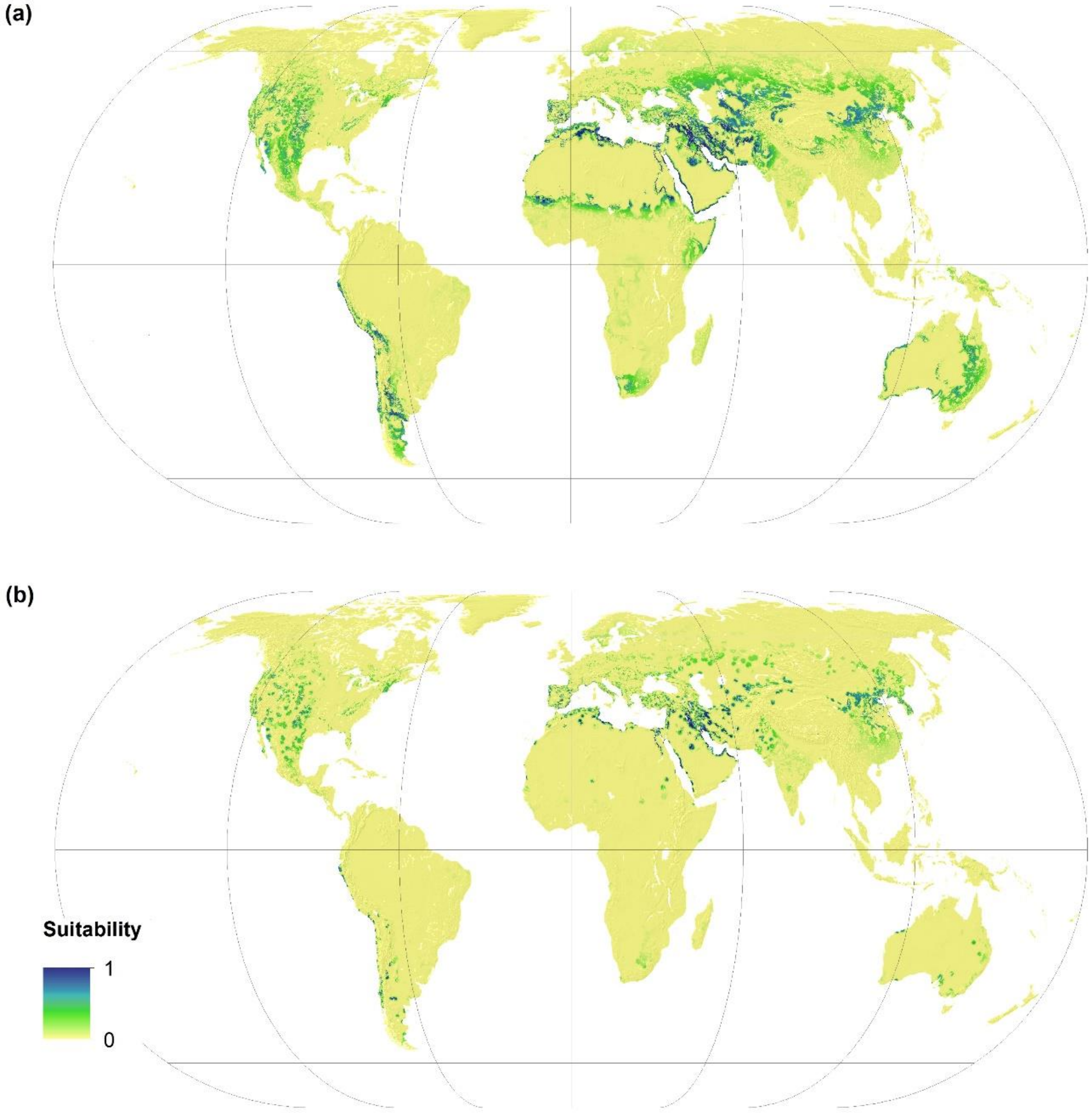

Figure 1. Global suitability map for microalgal biodiesel production based on the maximization of microalgal productivity, minimization of competition with food production, and minimization of direct impacts on biodiversity for (a) Scenario 1 (use of fresh, brackish or salt water without considering known industrial CO_2 sources) and (b) Scenario 2 (use of fresh, brackish or salt water adjacent to known industrial CO_2 sources).

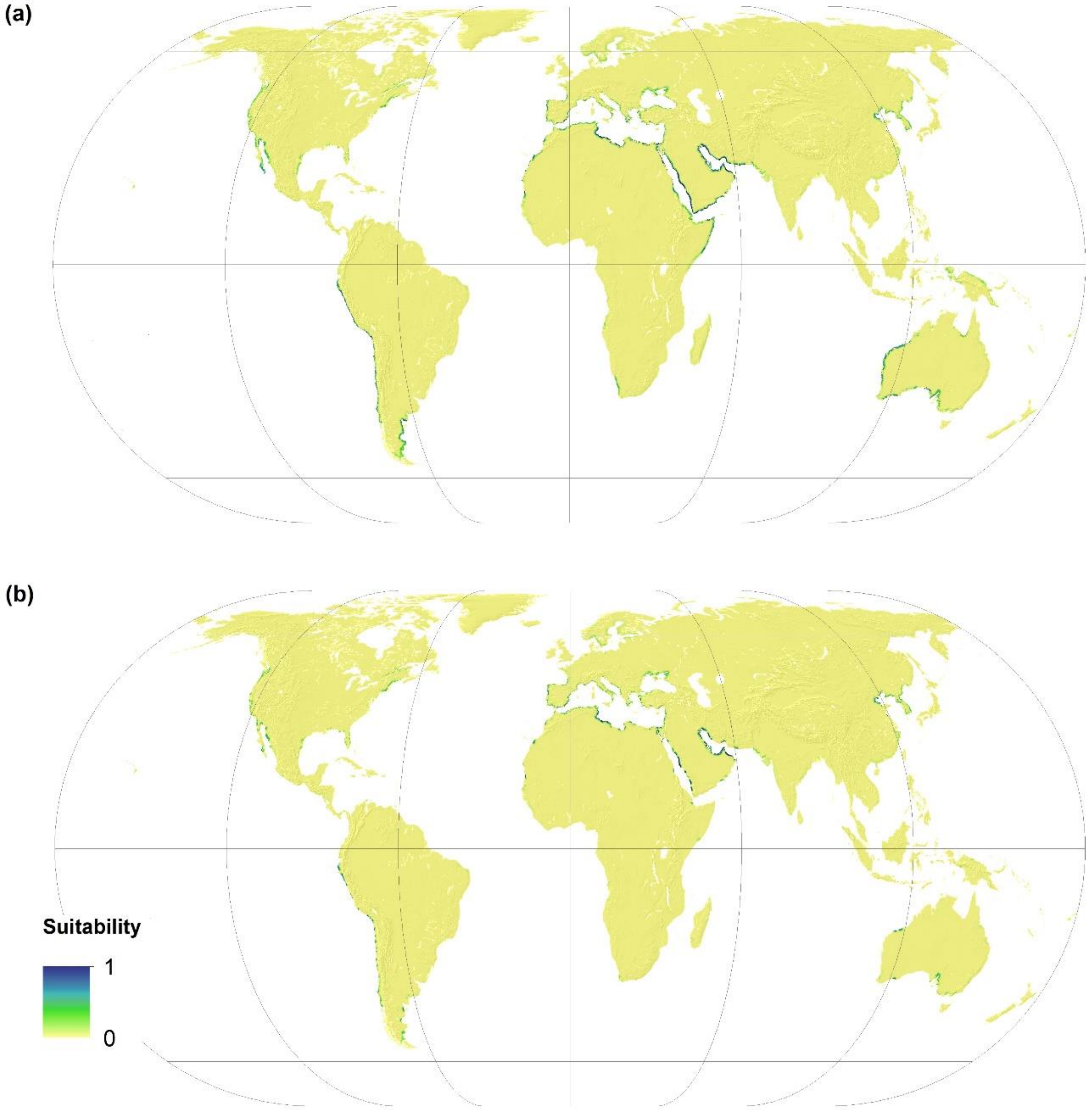

Figure 2. Global suitability map for microalgal biodiesel production based on the maximization of microalgal productivity, minimization of competition with food production, and minimization of direct impacts on biodiversity for (a) Scenario 3 (use of seawater without considering known industrial CO_2 sources) and (b) Scenario 4 (use of seawater adjacent to known industrial CO_2 sources).

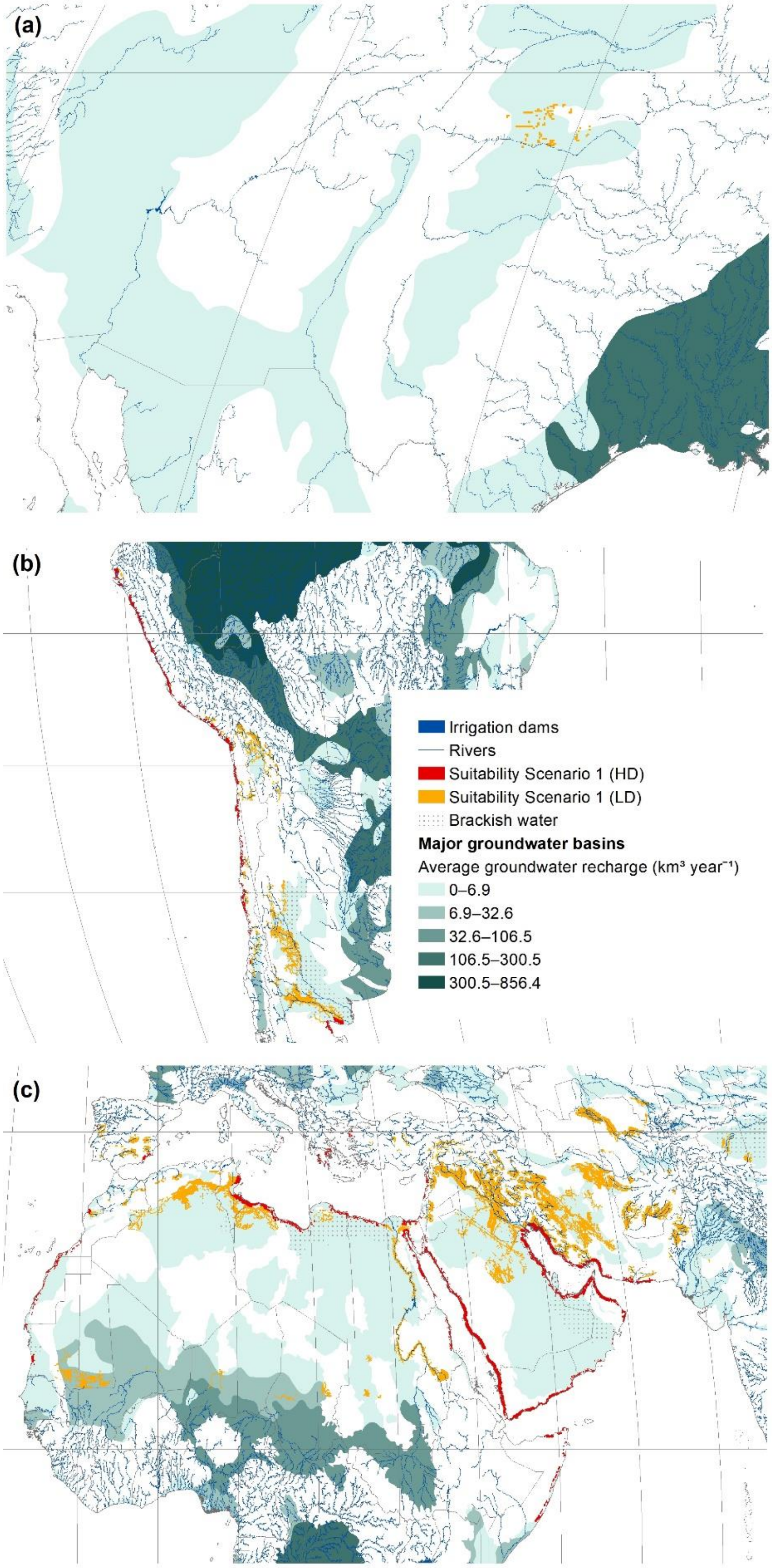

Figure 3. Top suitable areas for microalgal biodiesel production (suitability values ≥ 0.7) for Scenario 1 (use of fresh, brackish or salt water without considering known industrial CO2 sources) in (a) North America, (b) South America, (c) Southern Europe, North and East Africa, the Middle East, and South and Central Asia. Orange represents potential low-density microalgal cultivation (LD), dependent on fresh/brackish water availability, while red represents potential high-density microalgal cultivation (HD) based on seawater use.

Table 1. Land-cover composition within top suitable microalgal production lands (suitability values ≥ 0.7), based on the MODIS derived global mosaic for 2012 at a resolution of 5 arcminutes (Channan et al. 2014).

Land Cover	**Scenario 1**		**Scenario 2**		**Scenario 3**		**Scenario 4**	
	Area (thousands km^2)	Area (%)	Area (thousands km^2)	Area (%)	Area (thousands km^2)	Area (%)	Area (thousands km^2)	Area (%)
Barren or sparsely vegetated	850.9	59.8	266.2	57.4	239.4	78.4	102.7	77.3
Open shrublands	308.8	21.7	79.7	17.2	25.4	8.3	8.9	6.7
Grasslands	132.0	9.3	39.6	8.5	2.4	0.8	1.5	1.1
Croplands	87.4	6.1	61.4	13.2	9.2	3.0	7.7	5.8
Woody savannas	8.0	0.6	1.8	0.4	3.7	1.2	1.2	0.9
Cropland/Natural vegetation mosaic	5.8	0.4	1.9	0.4	2.1	0.7	1.2	0.9
Others	29.9	2.1	13.5	2.9	23.2	7.6	9.8	7.4
Total	1,422.8	100.0	464.2	100.0	305.3	100.0	132.9	100.0

For Scenarios 2, 3 and 4, which are the most feasible options for widespread microalgal biodiesel production in terms of reduced competition with scarce freshwater, 61%, 45% and 34% of top suitable lands (suitability values ≥ 0.7), respectively, fell within several politically unstable countries in Africa, the Middle East, and South Asia (i.e., Afghanistan, Egypt, Iran, Iraq, Lebanon, Libya, Mauritania, Niger, Pakistan, Somalia, Sudan, Syria, Turkey, and Yemen). Based on these scenarios, potential total microalgal biodiesel production ranged between 5.85×10^{11} and 1.81×10^{11} L year^{-1}, representing between 17% and 6% of total transport energy demands in 2016, respectively (Table 2). Among these scenarios, maximum levels of biodiesel production would be achieved in Scenario 2, followed by Scenarios 3 and 4, which are restricted to the use of seawater.

Table 2. Estimates of microalgal biodiesel production for Scenarios 2, 3 and 4 in top suitable microalgal production lands (suitability values ≥ 0.7) (see Supplementary Information for calculation details). The percentages of transport energy consumption fulfilled by each cultivation scenario are shown for 2016, 2030 and 2040. Scenarios of transport energy consumption (Current Policies Scenario, New Policies Scenario, and Sustainable Development Scenario) are based on the IEA (2017) energy production estimates.

		2016	**2030**			**2040**		
			Current Policies Scenario	**New Policies Scenario**	**Sustainable Development Scenario**	**Current Policies Scenario**	**New Policies Scenario**	**Sustainable Development Scenario**
Cultivation scenarios	**Potential biodiesel production (L year^{-1})**	**Shares (%)**						
Scenario 2	5.85×10^{11}	16.7	13.5	14.3	16.1	11.8	13.0	16.8
Scenario 3	4.17×10^{11}	11.9	9.7	10.2	11.5	8.4	9.3	12.0
Scenario 4	1.81×10^{11}	5.6	4.2	4.4	5.0	3.6	4.0	5.2

Less than 0.5%, 5.8%, 3.5%, and 5.1% of threatened amphibians, birds, mammals, and reptiles, respectively, would overlap top suitable microalgal production lands (i.e., suitability values ≥ 0.7) for Scenarios 2, 3, and 4. Around 25%, and less than 2.5%, 2.8%, and 3.6% of this set of threatened amphibians, birds, mammals, and reptiles, respectively, would face competition with microalgal production in more than 20% of their distribution ranges (Fig. 4). This competition would be highest for Scenario 3 compared to Scenarios 2 and 4 (Table S3).

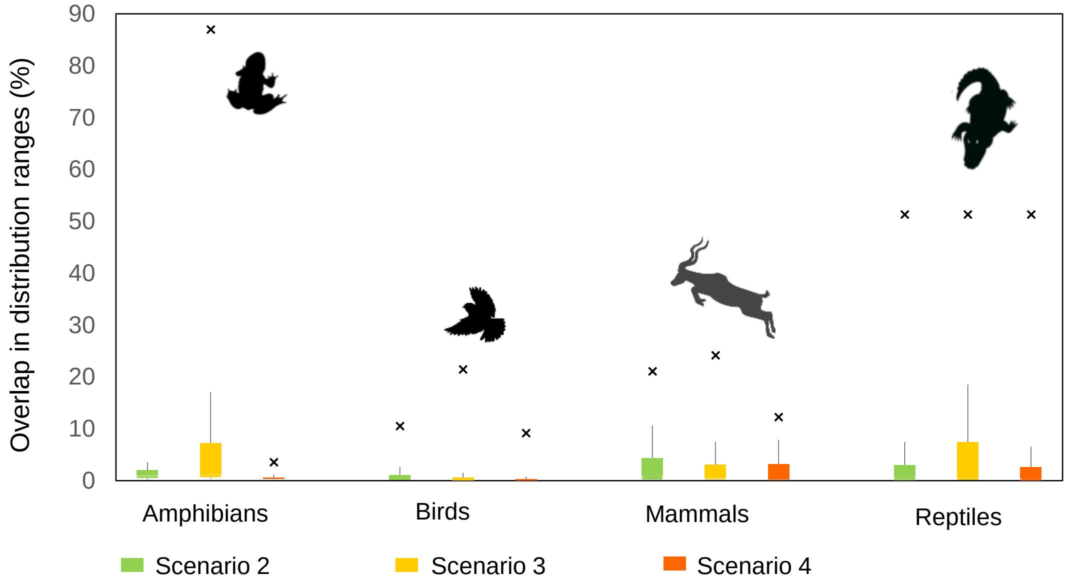

Figure 4. Boxplots showing the percentage of distribution ranges of threatened vertebrates (i.e., vulnerable, endangered, and critically endangered amphibians, birds, mammals, and reptiles) overlapping top suitable microalgal production lands (suitability values ≥ 0.7) based on Scenarios 2, 3, and 4. The maximum outliers were identified after multiplying the interquartile range by 1.5.

At a global scale, potential conflicts could arise among microalgal production and areas of high agricultural and biodiversity value, mainly in Central America, tropical and subtropical South America, Africa, India, and Southeast Asia (Fig. 5). If agricultural and biodiversity value are not considered, microalgal cultivation for one of the most feasible cultivation scenarios (i.e., Scenario 3, which is based on seawater) would include larger tracts of humid lands in the tropics (e.g., in Southeast Asian islands and Madagascar when just avoiding areas of high agricultural value; and in Central and South America, Southeast Africa, India, and Southeast Asian mainland when just avoiding areas of high biodiversity value) (Figs. 6, 7). Locations for microalgal cultivation would change as a function of targets in microalgal biofuel production (Figs. 8, 9). Potential conflicts with areas of higher agricultural and biodiversity value (e.g., in Central and South America, Africa, South and Southeast Asia, and China) would increase if fulfilling higher targets in microalgal biofuel demands (i.e., from 10% to 40% of total transport energy demands in 2016). Finally, more lands would be needed to fulfill higher targets in microalgal biofuel demands based on current and future energy consumption scenarios (IEA 2017) (Fig. 10).

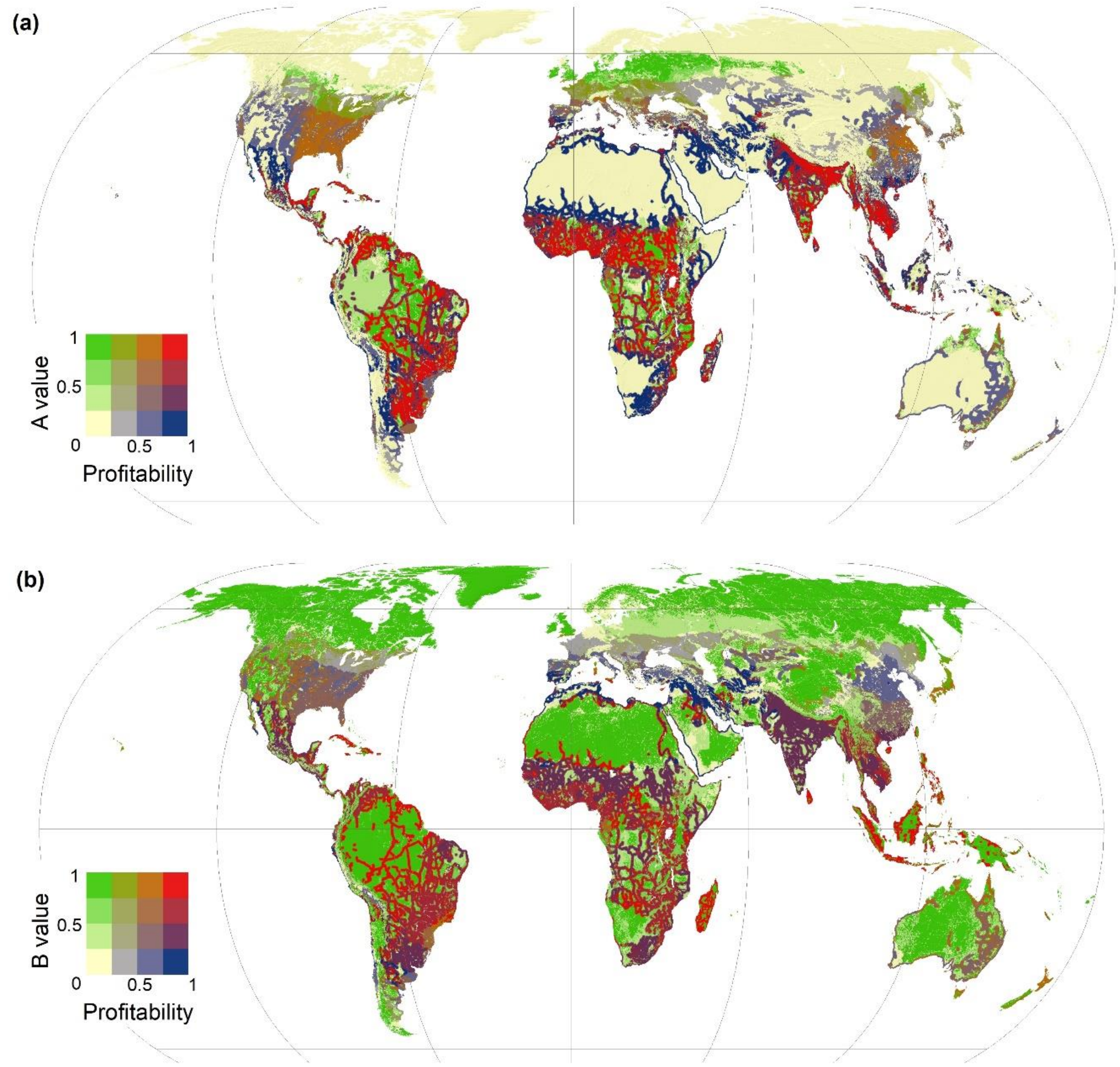

Figure 5. Overlapping of microalgal biodiesel profitability for Scenario 1 (i.e., use of fresh, brackish or salt water without considering known industrial CO_2 *sources) with (a) agricultural value, and (b) biodiversity value. The agricultural value corresponds to the potential gross economic rents from agricultural lands in USD* ha^{-1} *(Naidoo and Iwamura 2007). The biodiversity value (i.e., ranging from 0 to 1) is based on the number of vertebrate species (considering amphibians, birds, and mammals), the number of threatened vertebrate species (Jenkins et al. 2013), the presence of islands, and the presence of areas with low human pressures (Venter et al. 2016).*

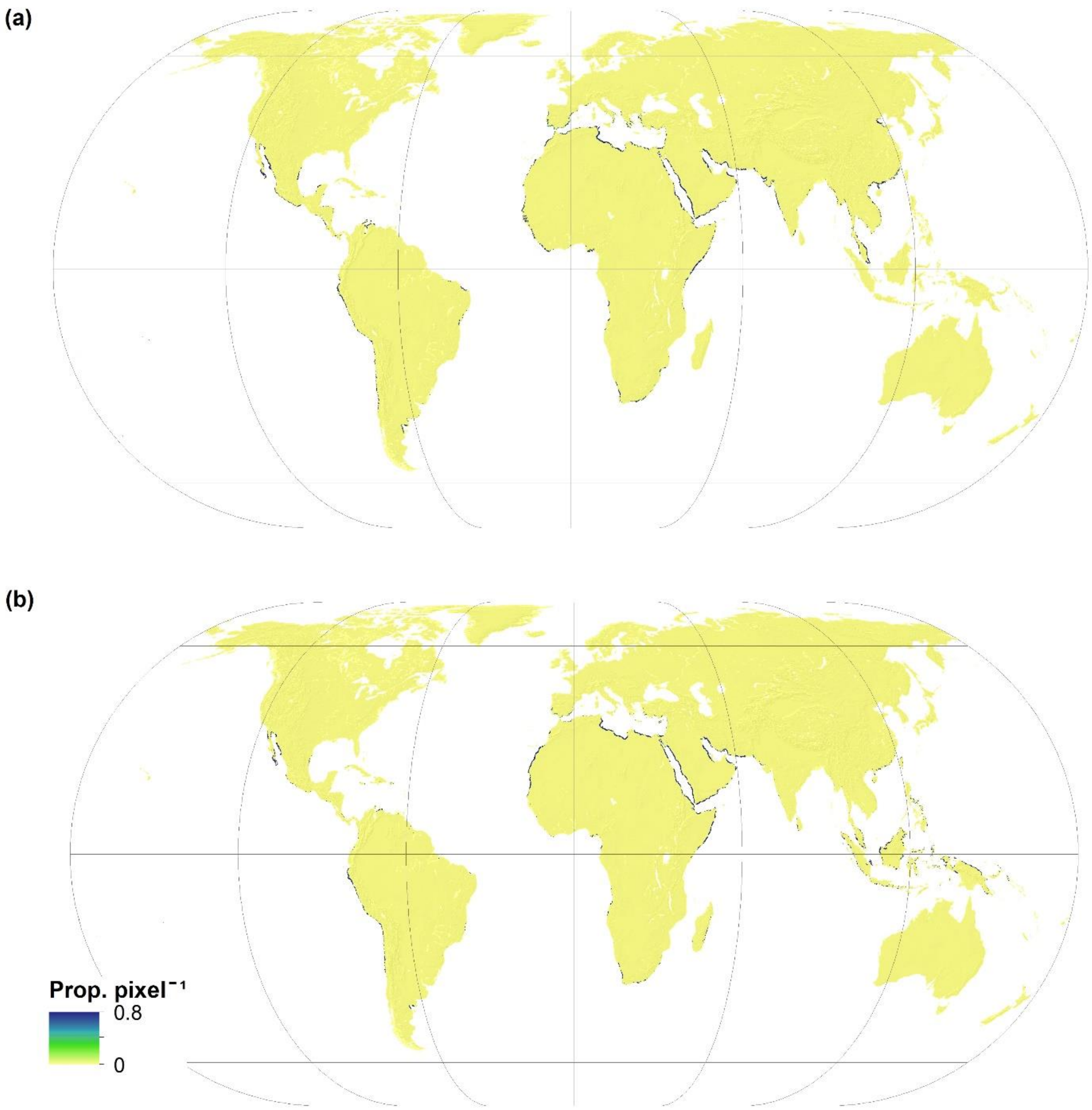

Figure 6. Microalgal cultivation areas for meeting 30% of global transport energy demand in 2016 for Scenario 3 (i.e., use of seawater without considering known industrial CO_2 sources). These areas were identified using an integer linear programming model (See Methods and Supplementary Information for details) and four sets of weights for agricultural value and biodiversity: (a) Maximization of profitability and minimization of direct competition with high-value agricultural lands and biodiverse areas, (b) Maximization of profitability and minimization of direct competition with high-value agricultural lands. Within each pixel (i.e., 25 km^2) a maximum proportion (Prop.) of 0.8 is permitted to be used for microalgal cultivation.

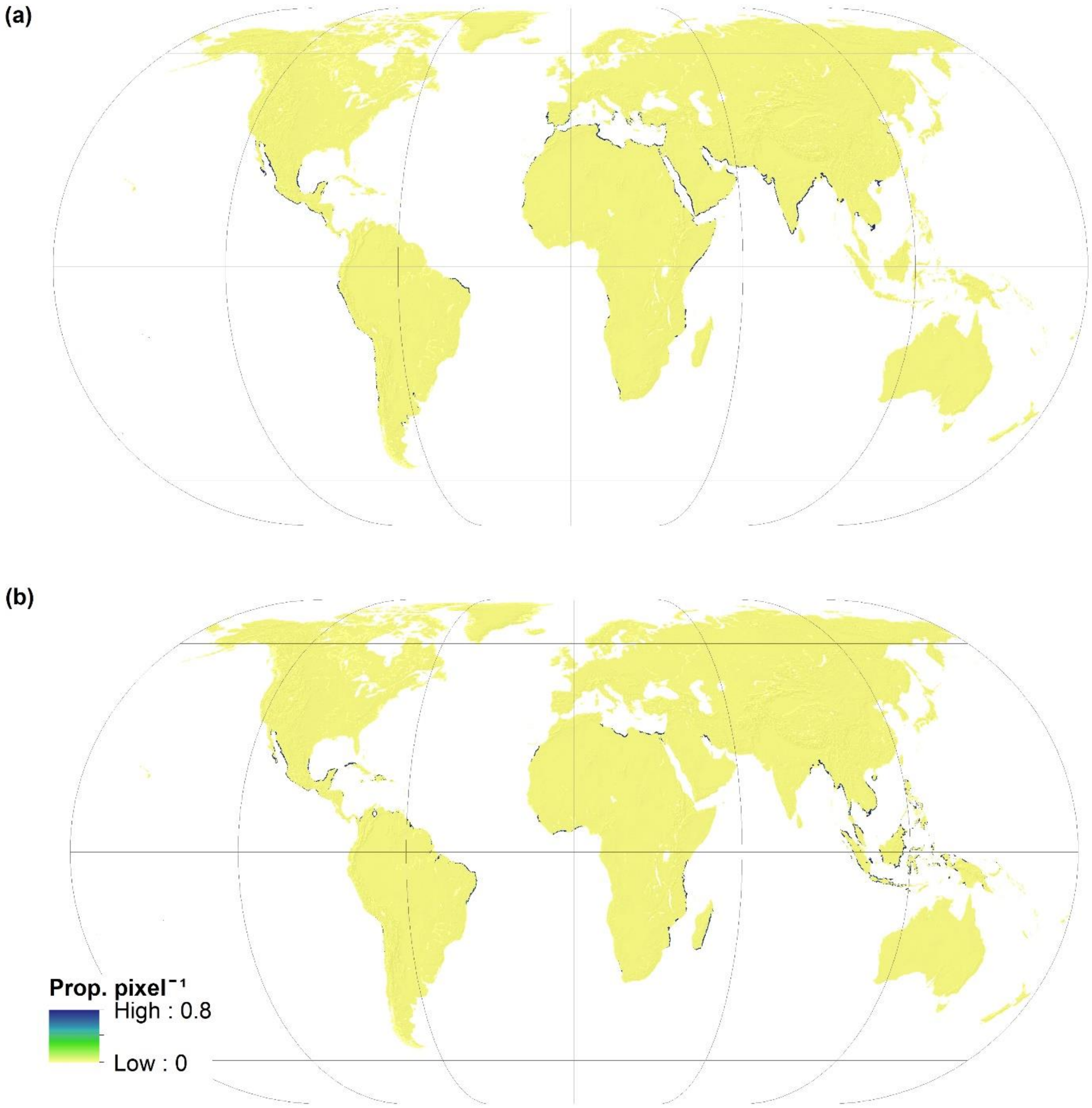

Figure 7. Microalgal cultivation areas for meeting 30% of global transport energy demand in 2016 for Scenario 3 (i.e., use of seawater without considering known industrial CO_2 sources). These areas were identified using an integer linear programming model (See Methods and Supplementary Information for details) and four sets of weights for agricultural value and biodiversity: (a) Maximization of profitability and minimization of direct competition with biodiverse lands, (b) Maximization of profitability irrespective of agricultural value or biodiversity. Within each pixel (i.e., 25 km^2) a maximum proportion (Prop.) of 0.8 is permitted to be used for microalgal cultivation.

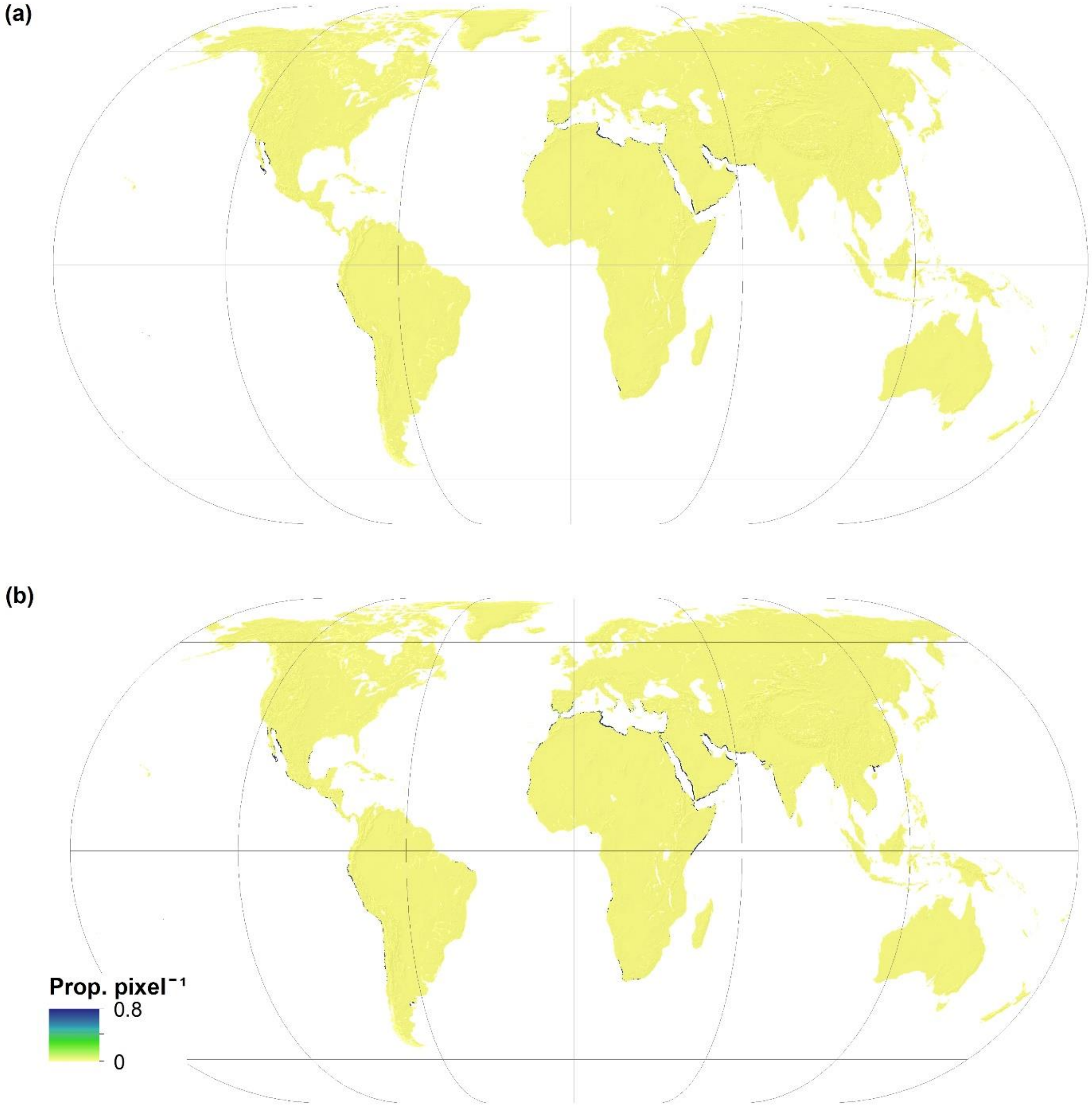

Figure 8. Microalgal cultivation areas for meeting (a) 10%, and (b) 20% of total transport energy demands in 2016 for Scenario 3 (i.e., use of seawater without considering known industrial CO$_2$ sources), identified using an integer linear programming model (See Methods and Supplementary Information for details). Within each pixel (i.e., 25 km^2) a maximum proportion (Prop.) of 0.8 is permitted to be used for microalgal cultivation.

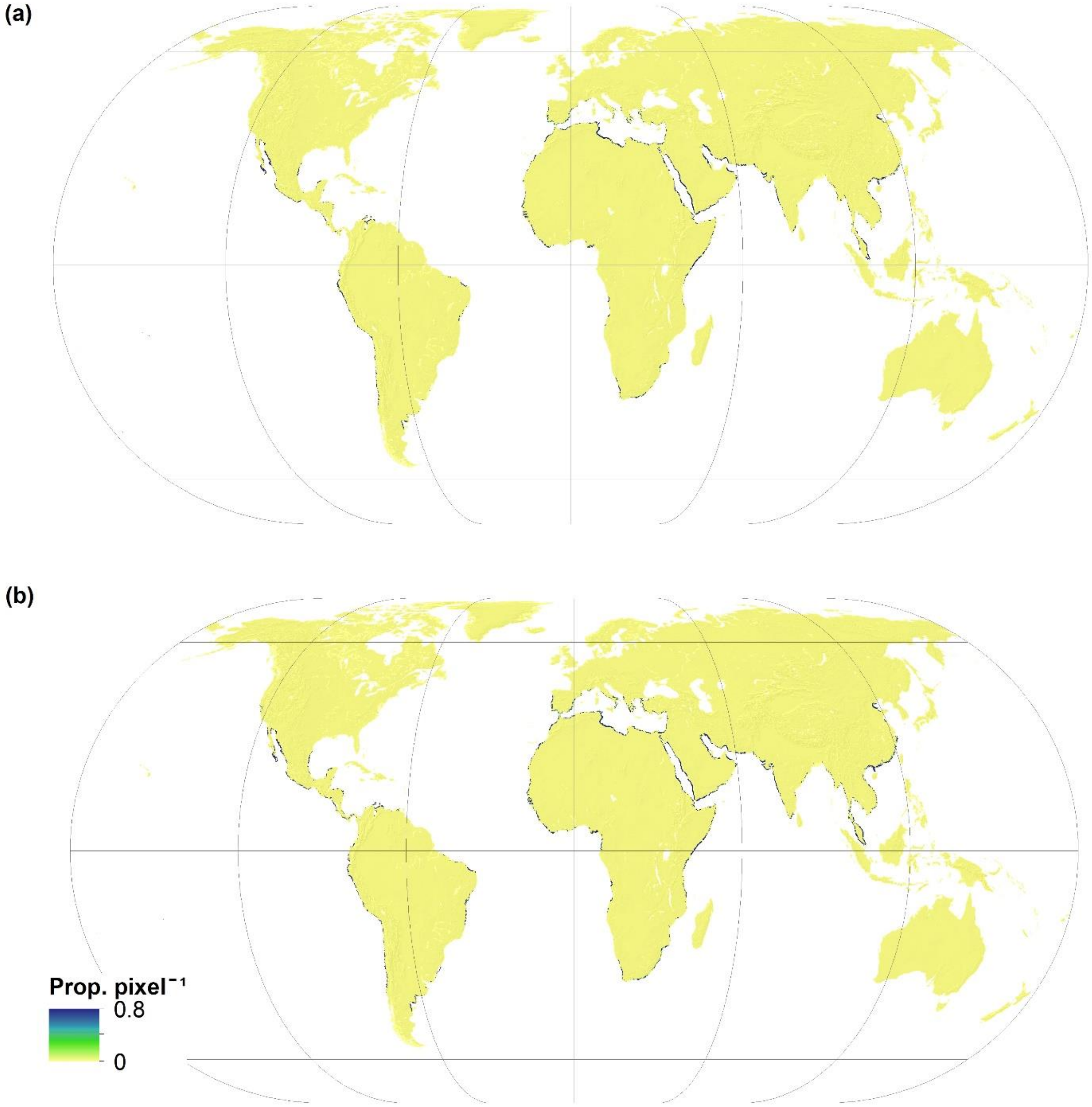

Figure 9. Microalgal cultivation areas for meeting (a) 30%, and (b) 40% of total transport energy demands in 2016 for Scenario 3 (i.e., use of seawater without considering known industrial CO_2 sources), identified using an integer linear programming model (See Methods and Supplementary Information for details). Within each pixel (i.e., 25 km^2) a maximum proportion (Prop.) of 0.8 is permitted to be used for microalgal cultivation.

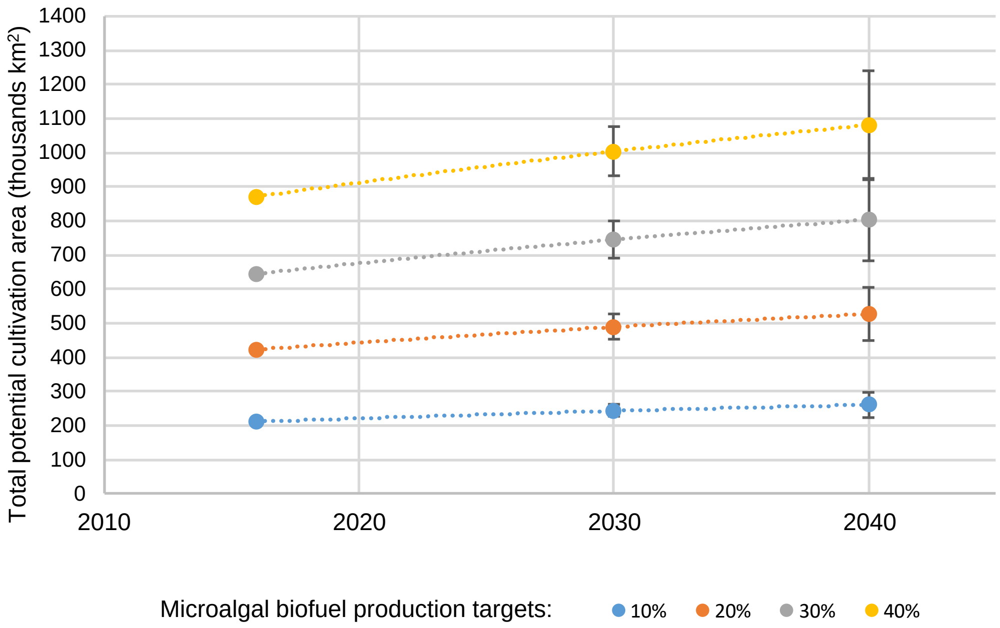

Figure 10. Potential microalgal cultivation area needed to meet 10%, 20%, 30% and 40% of total transport energy demands in 2016, 2030, and 2040. Scenarios for transport energy consumption (Current Policies Scenario, New Policies Scenario, and Sustainable Development Scenario) are based on the IEA (2017) energy production estimations. The average values among energy consumption scenarios are shown for each year with their standard deviations.

4. DISCUSSION

We provide the first global analyses on cost-effective areas for microalgal biodiesel production that minimize direct competition with food production and biodiversity, considering variables that increase the profitability in microalgal biofuel production. Our analyses are based on four scenarios for microalgal cultivation (i.e., use of fresh, brackish or salt water; use of fresh, brackish or salt water adjacent to known industrial CO_2 sources; use of seawater; use of seawater adjacent to known industrial CO_2 sources). Furthermore, we explore how microalgal production, agricultural value, and biodiversity are related, and how changes in current and future targets in energy demands alter the siting of microalgal production farms. These results can help in decision making towards the selection of best areas for microalgal biodiesel production at lower conflicts with food production and biodiversity.

Based on a multiple-criteria decision analysis (MCDA), our results show that dry tropical and subtropical mainlands in areas subject to high human pressures on the environment (i.e., human-transformed dry tropical and subtropical mainlands), are the most suitable areas for large-scale microalgal biodiesel production. While avoiding direct competition with agricultural and biodiverse lands (i.e., based on the richness of vertebrates, presence of threatened vertebrates, presence of islands, and presence of areas with low human pressures) these areas still provide access to water and flat lands for microalgal cultivation, access to transport networks that ensure supply of inputs and distribution of biodiesel, and low labor costs (here measured as GNI per capita) that reduce production costs. As expected, microalgal suitability increases where high solar irradiance and temperature facilitate larger microalgal biomass and lipid yields (Lundquist et al. 2010, Wigmosta et al. 2011, Quinn et al. 2012, Moody et al. 2014, Venteris et al. 2014), which occurs in tropical and subtropical regions of the world.

The use of dry lands for microalgal production, which in general are less suitable for cropping (Alexandratos and Bruinsma 2012) and hold lower biodiversity values compared to more humid regions (Gaston 2000), would decrease direct competition with high-value agricultural and biodiverse lands. In contrast, several studies developed in the USA show that humid regions are the most feasible locations for large-scale microalgal production (Wigmosta et al. 2011, Venteris et al. 2013, Coleman et al. 2014, Venteris et al. 2014). These studies indicate that the consumption of water per liter of microalgal oil and the costs associated with water pumping would be lower in the Southeastern USA (i.e., mainly around the Gulf and East Coasts) compared to the drier southwestern lands, where water demands and water pumping costs increase as a result of higher evaporation rates relative to precipitation. Notwithstanding, the use of humid areas for microalgal production would inevitably lead to direct competition with food production and biodiversity (although lower compared to first generation biofuels because of their higher biofuel productivities per unit area) (Correa et al. 2017). Furthermore, targeting humid areas for carbon sequestration, where forests can grow (Saatchi et al. 2011), is an effective solution for climate change mitigation (Canadell and Raupach 2008).

The establishment of low-density microalgal production farms would be a more sustainable option in regions where significant competition with freshwater resources is expected to occur, including dry areas around the Nile river in North Africa and the Tigris and Euphrates rivers in the Middle East, as well as along low-recharge aquifers in North America, South America, North and East Africa, Southern Europe, the Middle East, South and Central Asia, and China (Vorosmarty et al. 2010, Gleeson et al. 2012). Scenarios 3 and 4 (i.e., based on seawater use) would become a more feasible alternative for large-scale microalgal biodiesel production, in terms of reduced competition with scarce freshwater resources. However, top suitable lands (i.e., suitability values ≥ 0.7) would decrease from 1,422.8 thousand km^2 for Scenario 1 to 305.3 thousand km^2 and 132.9 thousand km^2 for Scenarios 3 and 4, respectively. In these areas, the use of microalgal strains tolerant to a wide range of salinity conditions could prevent the use of freshwater and minimize the use of seawater that would maintain pond salinities as water evaporates (Borowitzka and Moheimani 2013). Additionally, the recycling of harvest water could facilitate nutrient recovery while reducing water requirements (Yang et al. 2011, Venteris et al. 2013).

Currently not considered in other studies, the political stability of countries could constitute an additional challenge for the widespread adoption of microalgal biofuel production systems (i.e., between 61% and 34% of top suitable lands for Scenarios 2, 3, and 4 fell within politically unstable countries). However, several of these countries already have a well-developed infrastructure for oil production and processing (e.g., Egypt, Iran, Iraq, Libya, Sudan, and Turkey are among top oil producers globally), which would facilitate the transition towards a more sustainable future fuel production based on microalgae. Furthermore, microalgal biofuel production may represent an important development option to improve livelihoods and build sustainable economies in these countries, following the replacement of fossil fuels for limiting global warming (IPCC 2015). Microalgal production can lead to the creation of jobs for local communities, helping in poverty alleviation. The implementation of microalgal biorefinery systems that produce biofuels along with high-value products (e.g., food and animal feed) is of particular interest for increasing the profitability of microalgal production while offering economic opportunities for local communities and reaching regional and global targets in climate change mitigation, food demands, and agricultural production (Walsh et al. 2015, Correa et al. 2019).

Potential microalgal biodiesel production is a function of the cultivation scenarios and changes in membership midpoints applied to the different variables. Between 5.85×10^{11} and 1.81×10^{11} L year^{-1} could be produced in top suitable lands (suitability values ≥ 0.7) for the most feasible cultivation scenarios (i.e., Scenarios 2, 3, and 4). For these scenarios, changing the midpoint in slope from 5° to 15° would increase potential microalgal biodiesel production by between 8% and 10%, while decreasing the midpoint in lipid productivity from 13,000 to 7,800 L ha^{-1} year^{-1} (i.e., in 40%) would increase potential microalgal biodiesel production by between 8% and 32%, and increasing the midpoint in lipid productivity from 13,000 to 18,200 L ha^{-1} year^{-1} (i.e., in 40%) would decrease potential microalgal biodiesel production by between 45% and 82% (Figs. S6, S7 in Supplementary Information). Biodiesel production estimates are expected to increase with the cultivation of fast-growing and high-lipid producing microalgal strains (Mata et al. 2010, Slade and Bauen 2013, Ajjawi et al. 2017), along with the adoption of more efficient cultivation, harvesting, and processing techniques that increase microalgal biomass and lipid productivities (Pierobon et al. 2017, González-González et al. 2018). Reducing the uncertainty in global microalgal potential biodiesel production would require the refinement of models based on resource availability (e.g., inclusion of nutrients from wastewater sources, inclusion of CO_2 sources from anaerobic digesters, and inclusion of freshwater restrictions) and economic feasibility (e.g., considering land costs, opportunity costs with other economic activities, and several microalgal production technologies).

4.1 Relationships among microalgal production, agricultural value, and biodiversity value

Potential conflicts among microalgal production and areas of high agricultural and biodiversity value could arise within the tropical region (Fig. 5), which faces the highest deforestation rates globally as agricultural activities expand for meeting food and biofuel demands (Hansen et al. 2013, Laurance et al. 2014, Laurance 2015), in spite of harbouring most of Earth's biodiversity (Dirzo and Raven 2003, Kier et al. 2005). In fact, if agricultural and biodiversity values are not considered, microalgal production for Scenario 3 (i.e., use of seawater) would shift to areas of higher agricultural value and ecological importance (e.g., in Central and South America, Africa, India, and Southeast Asia), similarly to food crops for biofuel production. This would intensify the pressures on food production and biodiversity in regions currently impacted by agriculture and biofuel expansion, including the Southeast Asian tropical forests (Koh 2007, Fargione et al. 2010, Koh et al. 2011), as well as in regions with current little agricultural development such as the Amazon and Congo tropical forests (Laurance et al. 2001, Wich et al. 2014) and the South American and African savannas (Laurance 2015, Searchinger et al. 2015). Avoiding areas of high agricultural and biodiversity value for microalgal cultivation would help in decreasing direct competition with food production and biodiversity loss, which is unlikely by using food crops (Searchinger and Heimlich 2015, Correa et al. 2017).

The consideration of the trade-offs among microalgal biodiesel profitability, cultivation water source (i.e., fresh, brackish, and salt water) and its availability, along with the agricultural and biodiversity value of lands, could limit direct competition with food production and prevent further direct habitat loss in biodiverse regions (Correa et al. 2017). The use of human-transformed mainland coasts within the tropics and subtropics for microalgal production seems to be the most sustainable option in terms of reduced competition with freshwater resources, high-value agricultural lands, and biodiversity. However, dry coastal areas hold unique and threatened biodiversity (Durant et al. 2012, Brito et al. 2014, Vale et al. 2015, IUCN 2016) and provide a wide range of important ecosystem services (e.g., coastal protection, maintenance of fisheries, and tourism) (Barbier et al. 2011). In fact, top suitable microalgal production lands for Scenarios 2, 3, and 4 harbor as much as 3.1% of terrestrial threatened vertebrates globally (i.e., mainly birds and reptiles), and some of them would face competition with microalgal production in more than 20% of their distribution ranges (Table S3). Several of these areas could be easily avoided without significantly impacting species and microalgal production (i.e., for the amphibian *Eupsophus queulensis* and the Lima leaf-toed gecko, with distribution ranges smaller than 393.5 km^2). For species with larger distribution ranges (i.e., the Syrian hamster, the Atacama toad, the Peruvian plantcutter, the four-toed jerboa, and the rufous flycatcher, with distribution ranges larger than 4,713.6 km^2), microalgal cultivation could avoid their habitat patches. Furthermore, functional connections among dry terrestrial ecosystems and mangroves, mudflats, saltmarshes, and coral reefs (Martínez et al. 2007), should be preserved by avoiding pollution (e.g., through harvest water recycling).

4.2 Locations for siting microalgal farms for biodiesel production based on energy targets

Locations for microalgal biodiesel production would not only change as a function of trade-offs among profitability, water availability, agricultural value, and biodiversity but also along with targets in microalgal biofuel production. As expected, more lands would be needed to fulfill higher targets in microalgal biofuel demands. Furthermore, as targets in microalgal biofuels increase, regions of higher agricultural and biodiversity value would be considered suitable for microalgal cultivation. In fact, increasing microalgal production from fulfilling 10% to 40% transport energy demands in 2016, would lead to the inclusion of regions with higher agricultural and ecological importance within Central and South America, Africa, South and Southeast Asia, and China, potentially compromising food production and biodiversity in these areas.

Future assessments based on global and national targets in energy and food production, economic development (e.g., urbanization, mining, tourism), biodiversity conservation, and provision of ecosystem services (e.g., carbon sequestration and coastal protection), in the context of climate change, can improve the understanding of the socioeconomic and environmental role of microalgal biofuels. Spatially explicit comparisons with biofuel production alternatives (e.g., first and second generation biofuels), can guide the identification and adoption of more sustainable biofuel production systems (Correa et al. 2019). These comparisons can help to assess the impacts of microalgal biofuels in dry regions, in contrast to systems that rely on agricultural lands and more biodiverse areas for crop production (e.g., oil palm and sugarcane) (Jaiswal et al. 2017, Ocampo-Peñuela et al. 2018).

Although we propose that avoiding the cultivation of microalgae within agricultural and biodiverse areas would be the best option for reducing direct competition with food production and biodiversity, further assessments on the overall environmental impacts of microalgal production in humid areas are needed. These assessments could consider the replacement of areas of currently established biofuel crops by microalgal biofuel systems—which offer higher biofuel yields per unit area (Chisti 2008, Correa et al. 2017)—along with the co-location of microalgal systems with free nutrient sources (e.g., from wastewater and agricultural residues) (Fortier and Sturm 2012, Chiu and Wu 2013, Mu et al. 2014, Orfield et al. 2014, Roostaei and Zhang 2017) and free CO_2 sources (e.g., from industrial operations, including anaerobic digesters and biorefineries with fermenters) (Lundquist et al. 2010, Wigmosta et al. 2011, Orfield et al. 2014).

5. Concluding remarks

We propose best locations for siting microalgal farms for biodiesel production that meet substantial biofuel production levels while avoiding direct land-use competition with agricultural lands and biodiverse areas, through a GIS-based mutiple-criteria decision analysis and integer linear programming. We conclude that potential conflicts with food production and biodiversity conservation, as well as with freshwater consumption, can be reduced if cultivation is restricted to human-transformed dry mainland coasts in tropical and subtropical regions of the world, in contrast to first generation biofuels, which need agricultural lands and freshwater (Correa et al. 2017). However, even in these areas, the prevention of environmental impacts associated with microalgal production would be required. This includes halting direct habit loss for threatened species, by avoiding microalgal production within habitat patches while preserving functional connections among ecosystems (e.g., terrestrial dry ecosystems, mangroves, mudflats, saltmarshes, and coral reefs). Potential total biofuel production decreases with the accumulative number of constraints (i.e., from 5.85×10^{11} to 1.81×10^{11} L $year^{-1}$ for Scenarios 2 and 4, respectively, based on top suitable microalgal production lands). Locations for microalgal biodiesel production would not only change as a function of trade-offs between profitability, water availability, agricultural value, and biodiversity but also along with targets in microalgal biofuel production. Higher targets in microalgal biofuels would inevitably lead to competition with areas of higher agricultural and biodiversity value, mainly within the tropics and subtropics. Future assessments that include optimized cultivation technologies, cultivation of more productive microalgal strains, availability of nutrients (e.g., from wastewater sources and agricultural residues), availability of CO_2 (e.g., from anaerobic digesters), restrictions on freshwater use, regional changes in land costs, and trade-offs among ecosystem services (e.g., carbon storage and coastal protection), can further refine the assessment of opportunities for microalgal biofuel production at a global scale. Microalgal production could become an important economic alternative in areas with little potential for agricultural development and relatively low biodiversity value (i.e., human-transformed dry tropical and subtropical mainlands), thereby helping in poverty alleviation while reaching substantial energy and environmental targets.

ACKNOWLEDGMENTS

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Chapter 2. Supplementary Information

1. Development of suitability model for large-scale microalgal biodiesel production

Our model aimed at maximizing the profitability of microalgal biodiesel production while minimizing direct competition with food production and direct impacts on biodiversity (Fig. S1), based on four scenarios for microalgal cultivation: Scenario 1 (i.e., use of fresh, brackish or salt water), Scenario 2 (i.e., use of fresh, brackish or salt water adjacent to known industrial CO_2 sources), Scenario 3 (i.e., use of seawater), Scenario 4 (i.e., use of seawater adjacent to known industrial CO_2 sources).

Water availability, lipid productivity, availability of flat lands, proximity to transport networks (i.e., main roads and railroads), availability of low gross national income (GNI) per capita (used as a proximate for labor costs), and proximity to known industrial CO_2 sources were selected as the attributes for maximizing profitability. The potential annual gross economic rents from agricultural lands (Naidoo and Iwamura 2007) was selected as the attribute to minimize direct competition with food production, while the biodiversity value, based on the number of vertebrate species, number of threatened vertebrate species (Jenkins et al. 2013), presence of islands, and presence of areas with low human pressures (Venter et al. 2016) was selected as the attribute to minimize direct impacts on biodiversity.

Several suitability layers were developed to construct the final suitability model for each cultivation scenario. Fuzzy logic was applied to construct each layer, through the use of sigmoid or linear functions that transform entry values into suitability scores. This method allows the transformation of an input raster into a scale that ranges from 0 to 1, using a membership function. Following Raines et al. (2010) linear functions were defined as:

$$\mu(x) = 0 \; if \; x < min, \mu(x) = 1 \; if \; x > max$$

$$otherwise \; \mu(x) = \frac{(x - min)}{(max - min)}$$

Where x corresponds to each pixel value, max corresponds to the maximum value among pixels, and min corresponds to the minimum value among pixels.

Sigmoid functions with large membership (i.e., larger entry values result in high suitability values) were defined as:

$$\mu(x) = \frac{1}{1 + \frac{x^{-f_1}}{f_2}}$$

And sigmoid functions with small membership (i.e., smaller entry values result in high suitability values) were defined as:

$$\mu(x) = \frac{1}{1 + \frac{x^{f_1}}{f_2}}$$

Where f_1 is the spread of the function (defined as 5) and f_2 is the membership midpoint. The midpoints are assigned a suitability value of 0.5, and were defined based on the reviewed literature (Table S1).

These layers were overlaid for each of the four scenarios based on the Boolean AND/OR operators, using the software ArcGIS 10.5. While the AND operator retrieves the lowest value among layers (ensuring that pixels with the lowest values are maintained), the OR operator retrieves the highest value (ensuring that pixels with the highest values are maintained). This approach, based on set theory, allows the combining of the fuzzy layers without the use of weights.

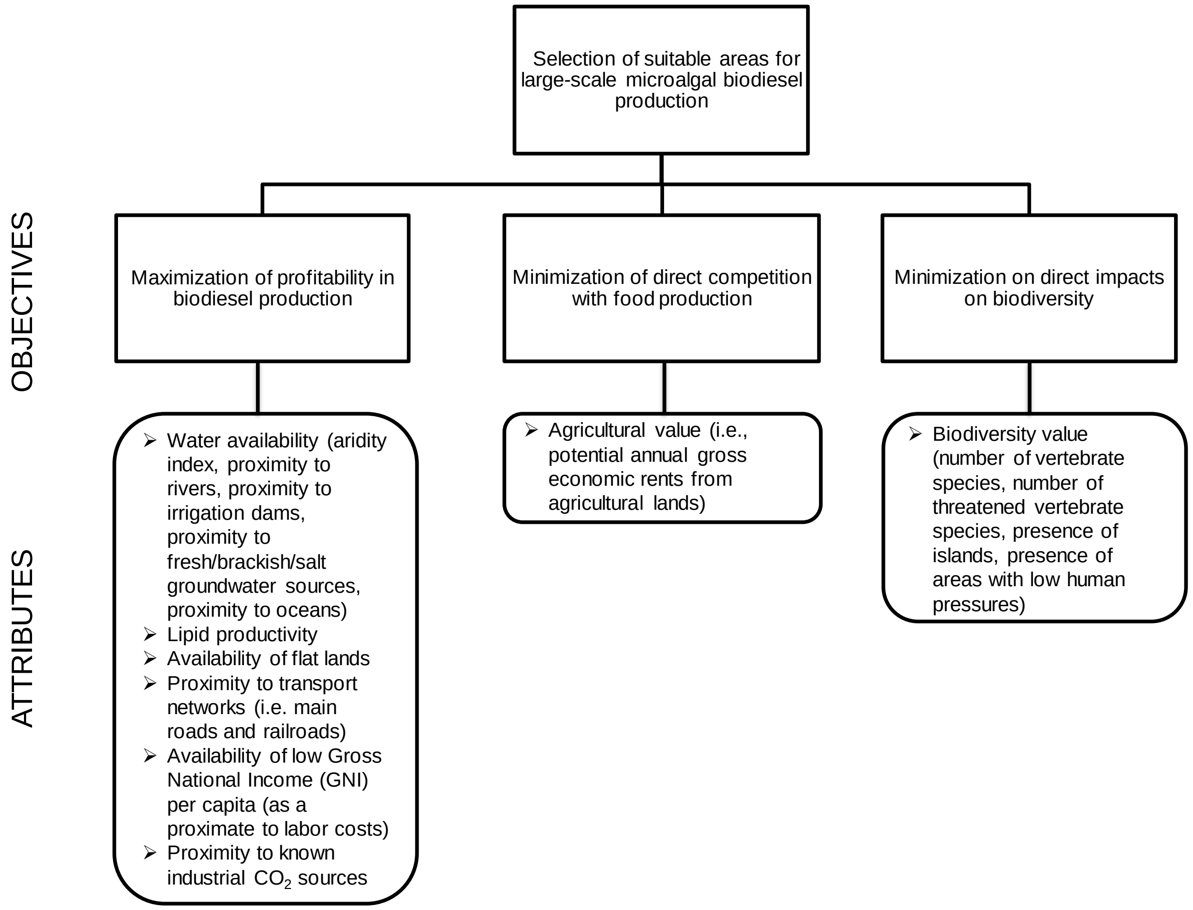


Figure S1. Set of criteria (objectives and attributes) for the development of a suitability model for siting microalgal farms for biodiesel production at a global scale, aiming at maximizing the profitability in microalgal production while minimizing direct competition with food production and direct impacts on biodiversity.

1.1 Construction of layers

A final suitability layer for microalgal biodiesel production was developed for each cultivation scenario, by overlying microalgal biodiesel profitability, agricultural value, and biodiversity value, based on the AND Boolean operator (Figs S2, S3, S4, and S5). Protected areas, Key Biodiversity Areas (KBA) (BirdLife International 2016), water bodies (Lehner and Döll 2004) and urban areas (Schneider et al. 2009) were excluded from the analyses, assigning No Data to water bodies and zero to the other layers. Protected areas corresponded to the IUCN categories Ia, Ib, II, III, IV, V and VI (i.e., strict nature reserves, wilderness areas, national parks, natural monument or features, habitat/species management areas, protected landscapes, and protected areas with sustainable use of natural resources), as well as areas where no category has been reported or assigned or where the IUCN categories do not apply (i.e., world heritage sites and UNESCO MAB reserves) (UNEP-WCMC 2016). KBA included important areas for the conservation of biodiversity and threatened species (BirdLife International 2016). Water bodies corresponded to large lakes and reservoirs with surface areas ≥ 100 km^2 (Lehner and Döll 2004), while urban areas were obtained from the classification developed by Schneider et al. (2009) for built environments.

1.1.1 Microalgal profitability

Microalgal profitability was the result of overlaying water availability (i.e., fresh, brackish, or salt water sources for Scenarios 1 and 2, and proximity to oceans for Scenarios 3 and 4), along with lipid productivity, availability of flat lands, proximity to transport networks (i.e., main roads and railroads), availability of low gross national income (GNI) per capita, and proximity to known industrial CO_2 sources (for Scenarios 2 and 4), using the AND Boolean operator. Information for agricultural CO_2 sources (e.g., from anaerobic digesters, fermenters in biorefineries, etc) was not available globally and thus not included in the present study.

For Scenarios 1 and 2, the aridity index, proximity to rivers, proximity to irrigation dams, proximity to fresh, brackish, or salt groundwater sources, and proximity to oceans were overlaid using the OR Boolean operator. A recharge/discharge ≥ 1.8 km^3 $year^{-1}$ was used for selecting suitable rivers, irrigation dams, and groundwater basins. This amount of water could sustain nearly 80 km^2 of microalgal open ponds (i.e., around twenty 400-ha microalgal ponds) in regions with high evaporative loss (i.e., 2,000 mm $year^{-1}$) and compromise 10% of total available water per year if harvest water is recycled. In areas with lower evaporation loss (e.g., 1,000 mm $year^{-1}$) a similar water recharge/discharge could sustain nearly 140 km^2 of microalgal ponds (i.e., around thirty-five 400-ha microalgal ponds) if harvest water is recycled. This is considering that a microalgal production farm consisting of 400 ha raceway ponds with a depth of 30 cm (Lundquist et al. 2010, Wigmosta et al. 2011) would need a constant volume of around 0.0012 km^3 $year^{-1}$, which should be continuously replaced because of evaporative loss (Gerbens-Leenes et al. 2014). For groundwater resources an estimation of the annual water recharge was calculated for each aquifer mapped in the Whymap database (BGR & UNESCO 2008), multiplying the average water recharge (mm $year^{-1}$) within categories by their area. Based on the river bankfull width database developed by Andreadis et al. (2013), streams with bankfull width equal or higher than 54.4 m were selected (as having a mean annual peak discharge equal or higher than 57.08 m^3 s^{-1}, which corresponds to 1.8 km^3 $year^{-1}$). Mean annual discharge is by definition lower than mean annual peak discharge, which would further restrict available water from rivers for microalgal cultivation. The development of a high-resolution database on mean annual river discharge would help to refine estimates on freshwater availability.

Lipid productivity was predicted globally through a multiple linear regression model, based on 4,388 lipid productivity estimates for the cultivation of *Nannochloropsis* sp. in photobioreactors (Moody et al. 2014), using the package "raster" (Hijmans et al. 2017) in the software R 3.4.2. To our knowledge, these are the best available estimates on microalgal biomass and lipid productivities at a global scale, subject to further refinements as strains with different lipid contents and preferences in growing conditions are considered (Richmond 1986, Ras et al. 2013, Singh and Singh 2015). Additionally, these productivity estimates are similar to values already achieved for other species in open raceway ponds (Schenk 2016). Mean annual radiation and the residuals of mean annual temperature explained by radiation (Hijmans et al. 2005, Fick and Hijmans 2017) were used as explanatory variables. This allowed the prediction of lipid productivities in areas with lower densities of point estimates, such as mountainous areas, accounting for the geographic variation in radiation and temperature. 89% of the variance was explained by the model (i.e., adjusted R-squared = 0.8848) (Table S2). The Pearson's r correlation coefficient between original productivity values and predicted productivity values was 0.94 ($t = 180.79$, $df = 4{,}254$, $p\text{-value} < 2.2 \times 10^{-16}$).

The proximity to rivers, irrigation dams, fresh/brackish/salt groundwater sources, oceans, transport networks, and known industrial CO_2 sources, was calculated based on a cost layer (i.e., cost distance). For constructing the cost layer, the slope was rescaled using a linear function with output values ranging from 1 to 10. This allowed the inclusion of slope as a physical constraint for accessing resources (i.e., water and CO_2) and transport networks.

1.1.2 Agricultural and biodiversity value

Agricultural value corresponded to the potential annual gross economic rents from agricultural lands estimated by Naidoo and Iwamura (2007). Biodiversity value was obtained by overlaying the number of vertebrates species (i.e., amphibians, birds, and mammals), the number of threatened vertebrates (i.e., vulnerable, endangered, or critically endangered amphibians, birds, and mammals) (Jenkins et al. 2013), the presence of islands (as a proximate variable to vulnerable areas with endemic populations/species), and the presence of areas with low human pressures (which is related to the integrity of ecosystems) (Venter et al. 2016), using the AND Boolean operator.

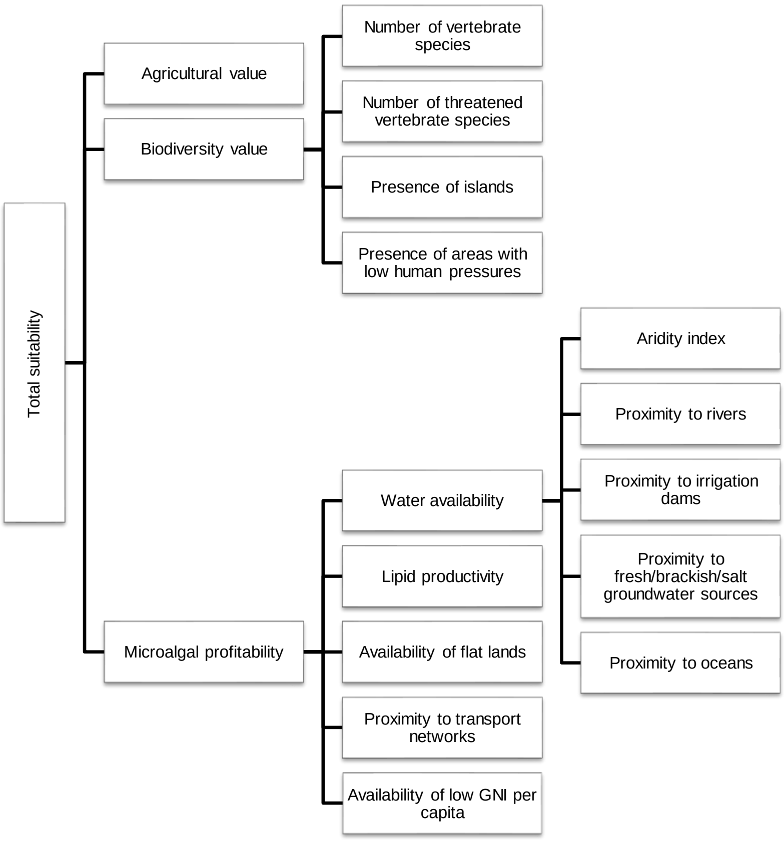


Figure S2. Overlaying of suitability layers for the development of a suitability model for siting microalgal farms for biodiesel production at a global scale. Scenario 1: Use of fresh, brackish or salt water without taking into account known industrial CO_2 sources.

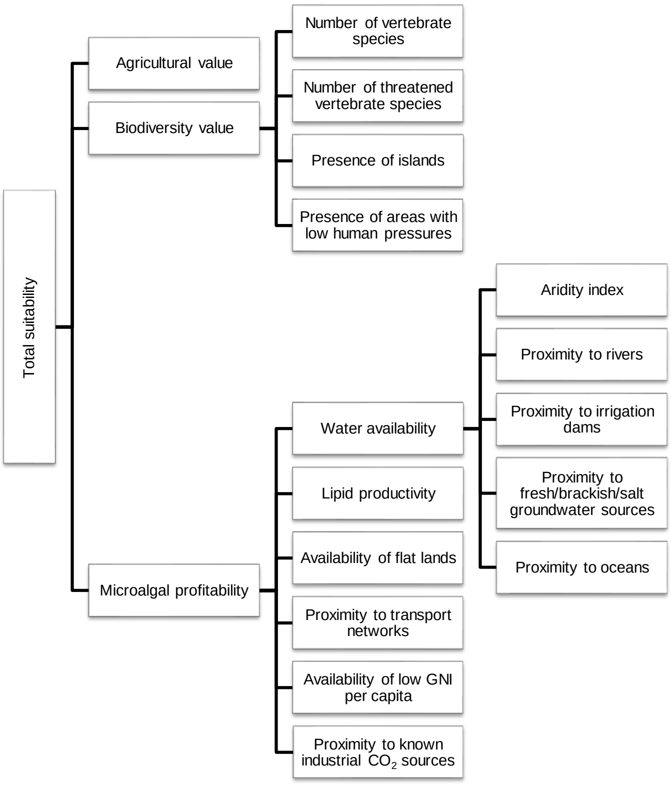


Figure S3. Overlaying of suitability layers for the development of a suitability model for siting microalgal farms for biodiesel production at a global scale. Scenario 2: Use of fresh, brackish or salt water adjacent to known industrial CO_2 sources.

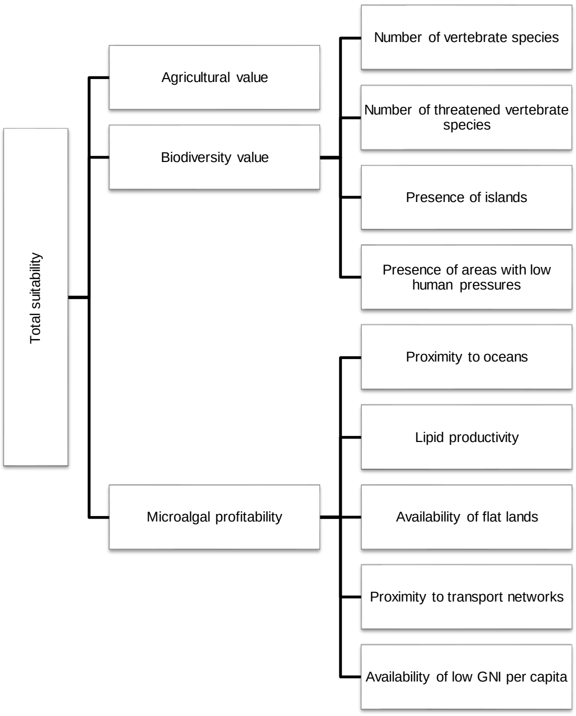


Figure S4. Overlaying of suitability layers for the development of a suitability model for siting microalgal farms for biodiesel production at a global scale. Scenario 3: use of seawater without taking into account known industrial CO_2 *sources.*

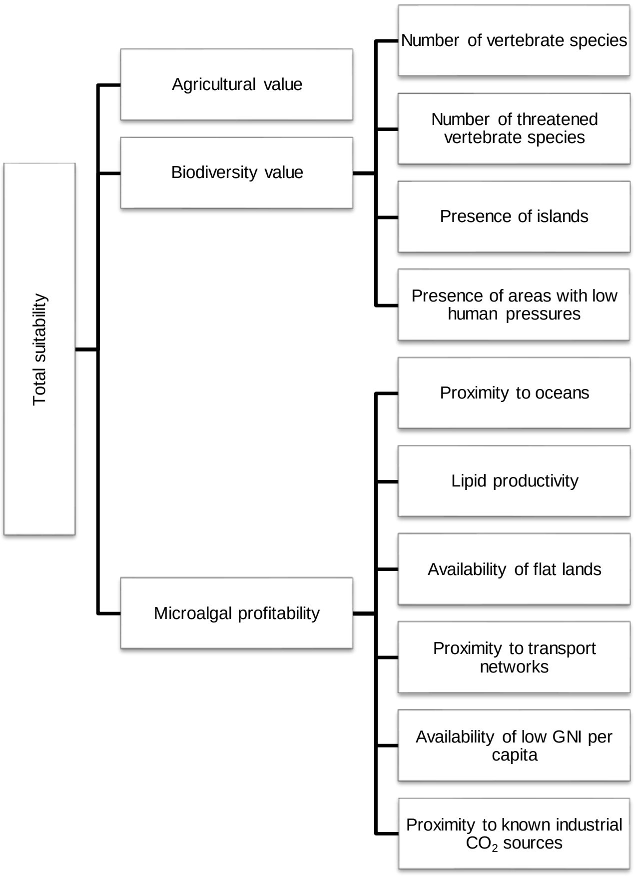


Figure S5. Overlaying of suitability layers for the development of a suitability model for siting microalgal farms for biodiesel production at a global scale. Scenario 4: Use of seawater adjacent to known industrial CO_2 *sources.*

1.1.3 Projection of rasters

All rasters were transformed into the Eckert-IV equal-area pseudocylindrical map projection. Rasters with spatial resolution coarser than 5 × 5 km (i.e., known industrial CO_2 sources, potential annual gross economic rents from agricultural lands, number of vertebrate species, and number of threatened vertebrate species) were resampled. The Nearest Neighbor resampling method was applied for the known industrial CO_2 sources and for the potential annual gross economic rents from agricultural lands. This method is suitable for categorical data and does not change pixel values. The Bilinear Interpolation resampling method was applied for the number of vertebrate species and for the number of threatened vertebrate species. This method is suitable for continuous data and creates new values based on surrounding pixels.

Table S1. Original layers and fuzzy membership functions applied for the construction of suitability layers. Sigmoid Large: larger entry values result in high suitability. Sigmoid Small: smaller entry values result in high suitability. Not Applicable (NA).

Objectives	Layers	Description	Original spatial resolution for rasters	Type of membership function	Membership midpoint	Source
Maximization of profitability in biodiesel production	Aridity index	Quantification of precipitation availability over atmospheric water demand. AI = MAP/MAE, where AI corresponds to the aridity index, MAP corresponds to mean annual precipitation and MAE corresponds to mean annual potential evapotranspiration.	30 arcseconds	Sigmoid Large	1	Global aridity and PET database (Trabucco and Zomer 2009)
	Proximity to rivers	Cost distance to permanent rivers with annual discharge ≥ 1.8 km^3 year^{-1}. Based on annual peak discharge.	NA	Sigmoid Small	50 km	Layer based on HydroSHEDS (Lehner et al. 2008), Vmap0 for permanent streams http://gis-lab.info/qa/vmap0-eng.html and river bankfull width database (Andreadis et al. 2013)
	Proximity to irrigation dams	Cost distance to irrigation dams with annual recharge ≥ 1.8 km^3 year^{-1}	NA	Sigmoid Small	50 km	GRanDv1 database (Lehner et al. 2011)
	Proximity to fresh/brackish/ salt groundwater sources	Cost distance to fresh/brackish/salt aquifers with annual recharge ≥ 1.8 km^3 year^{-1}. Excludes areas with complex hydrogeological structures, and areas with local and shallow aquifers.	NA	Sigmoid Small	50 km	Groundwater Resources of the World 1: 25 000 000. (BGR & UNESCO 2008)
	Proximity to oceans	Cost distance to oceans	NA	Sigmoid Small	50 km	Oceans v.3.00 http://www.naturalearthdata.com
	Lipid productivity	Lipid productivity based on 4,388 lipid point estimates for the cultivation of *Nannochloropsis* sp. in photobioreactors (Moody et al. 2014), using as predictors mean annual radiation and the residuals of mean annual temperature explained by radiation	5 × 5 km	Sigmoid Large	13,000 L ha^{-1} year^{-1}	Layer based on lipid productivity estimates (Moody et al. 2014), and WorldClim v.1.4 and v2 (Hijmans et al. 2005, Fick and Hijmans 2017)
	Availability of flat lands	Terrain slope	30 arcseconds	Sigmoid Small	5°	Layer derived from GTOPO30 DEM https://lta.cr.usgs.gov/GTOPO30
	Proximity to transport networks	Cost distance to roads and railroads	NA	Sigmoid Small	50 km	Roads and railroads v. 3.0.0 http://www.naturalearthdata.com
	Availability of low gross national income (GNI) per capita	GNI per capita, Atlas method in 2014. Proximate variable for labor costs.	NA	Linear (inverse)	NA	GNI per capita database (World Bank 2015)
	Proximity to known industrial CO$_2$ sources	Cost distance to known industrial CO$_2$ sources in 2010, including public electricity and heat production, manufacturing industries and construction, production of minerals, production of metals (IPCC codes 1A1a, 1A2, 2A, 2C) with CO$_2$ emissions ≥ 10 µg m^{-2} s^{-1}	360 arcseconds	Sigmoid Small	50 km	Global Emissions EDGAR v4.2 FT2010 (European Commission 2011)
Minimization of direct competition with food production	Agricultural value	Potential annual gross economic rents from agricultural lands	300 arcseconds	Sigmoid Small	USD 200 ha^{-1} year^{-1}	Potential annual gross economic rents from agricultural lands (Naidoo and Iwamura 2007)
	Number of vertebrate species	Number of vertebrate species (amphibians, birds, and mammals) based on IUCN species distribution maps, Bird Life International, and Nature Serve	10 × 10 km	Sigmoid Small	230 species	Biodiversity maps (Jenkins et al. 2013)

Minimization of direct impacts on biodiversity	Number of threatened vertebrate species	Number of threatened vertebrate species (amphibians, birds, and mammals) based on IUCN distribution maps, Bird Life International, and Nature Serve	10 × 10 km	Sigmoid Small	15 species	Biodiversity maps (Jenkins et al. 2013)
	Presence of islands	Islands	NA	Sigmoid Large	1,000,000 km^2	Layer based on GADM database *http://gadm.org/*
	Presence of areas with low human pressures	Measure of human pressures (no pressure, low pressure, moderate pressure, high pressure, very high pressure) based on the presence of built environments, croplands, pastures, human population density, night-time lights, railways, roads, and navigable waterways	1 × 1 km	Sigmoid Large	4	Human footprint (Venter et al. 2016)

Table S2. Fitted model between lipid productivity, mean annual radiation and the residuals of mean annual temperature explained by radiation (i.e., sequential regression) as predictor variables (Dormann et al. 2013), based on 4388 lipid point estimates for the cultivation of Nannochloropsis sp. *in photobioreactors (Moody et al. 2014).*

Coefficients	Estimate	Std. Error	t value	P value
Intercept	-6.56	1.17×10^{-1}	-56.09	$<2 \times 10^{-16}$ ***
Radiation	1.40×10^{-3}	7.75×10^{-6}	180.69	$<2 \times 10^{-16}$ ***
Residuals of temperature explained by radiation	2.65×10^{-2}	4.46×10^{-4}	59.38	$<2 \times 10^{-16}$ ***

Residual standard error: 1.587 on 4253 degrees of freedom (72 observations deleted due to missingness)

Multiple R-squared: 0.8848, Adjusted R-squared: 0.8848

F-statistic: 1.634×10^4 on 2 and 4253 DF, p-value: $<2 \times 10^{-16}$

2. Calculation of microalgal biodiesel production

Total potential biodiesel production was calculated for top suitable microalgal production lands (suitability values ≥ 0.7) based on the most feasible microalgal cultivation scenarios (Scenarios 2, 3, and 4) based on the following equation:

$$B = P * 0.8 * 0.81$$

where B corresponds to biodiesel production (L year^{-1}), P corresponds to the summation in estimated microalgal lipid productivity per pixel within top suitable microalgal production lands (L year^{-1}) (Moody et al. 2014), 0.8 is the assumed proportion of area that could be used for cultivation while 0.2 would remain as associated infrastructure (Wigmosta et al. 2011), and 0.81 is the assumed proportion of biodiesel produced from an initial volume of lipids contained in microalgal cells (i.e., the product of the lipid extraction efficiency from microalgal cells, 0.9, and the lipid conversion efficiency into biodiesel, 0.9).

The percentage of global transport energy demands that could be fulfilled by each of the four microalgal biodiesel production scenarios was calculated by dividing the total energy yields (GJ year^{-1}) in top suitable lands by the transport energy demands in 2016, 2030 and 2040 (GJ year^{-1}) (IEA 2017), and then multiplying by 100. Energy yields for each scenario (GJ year^{-1}) were obtained by multiplying the biodiesel production B (L year^{-1}) by 0.0326 GJ L^{-1} (i.e., low heating value, which is closest to the actual energy yield in motor vehicles) (Hofstrand 2008). Transport energy demands were converted into GJ from million tonnes of oil equivalent (MTOE) by multiplying by the conversion factor 4.1868×10^7 GJ MTOE^{-1} (IEA 2017).

3. Sensitivity analysis of microalgal biodiesel production

A sensitivity analysis was developed based on slope and lipid productivity, in order to determine how changes in model parameters influence the siting of microalgal production farms and biodiesel production. The slope was increased from a membership midpoint of 5° to 10° and 15°; and lipid productivity was both increased and decreased in 20% and 40% from a midpoint of 13,000 L ha^{-1} year^{-1}, using the one-at-a-time method, in which changes in values for each factor are evaluated in turn (Malczewski and Rinner 2015). Results show that changes in midpoints for lipid productivity are more important than changes in midpoints for slope in estimating potential microalgal production areas and biodiesel yields (Figs S6 and S7).

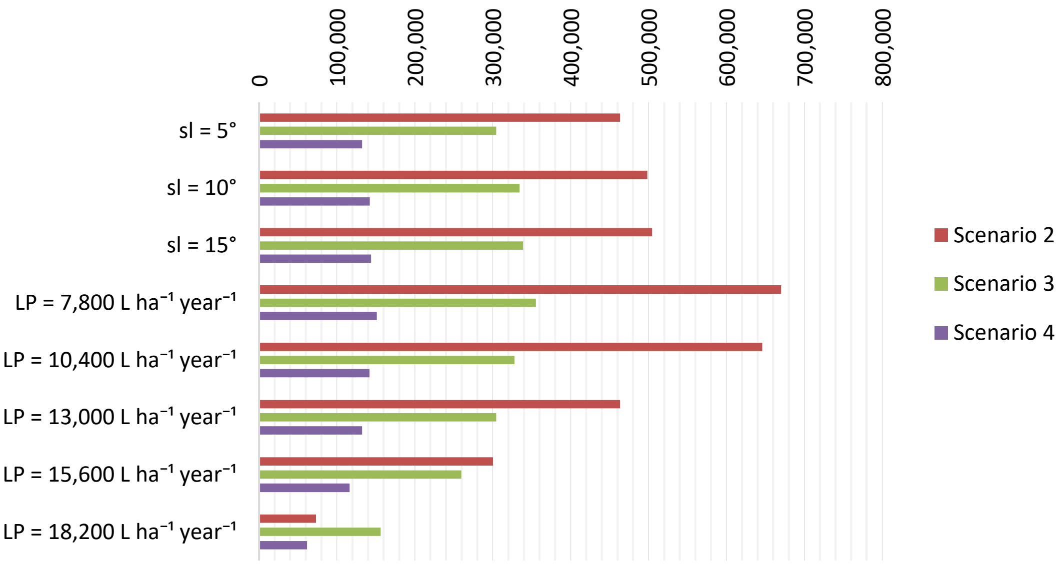


Figure S6. Sensitivity analyses on potential microalgal production area (km^2) for Scenarios 2, 3 and 4 considering top suitable lands (suitability values ≥ 0.7). Scenario 2: use of fresh, brackish or salt water adjacent to known industrial CO_2 sources. Scenario 3: use of seawater without taking into account known industrial CO_2 sources. Scenario 4: use of seawater adjacent to known industrial CO_2 sources. The slope (sl) was increased from a membership midpoint of 5° to 10° and 15°. Lipid productivity (LP) was both increased and decreased by 20% and 40% from a midpoint of 13,000 L ha^{-1} year^{-1}.

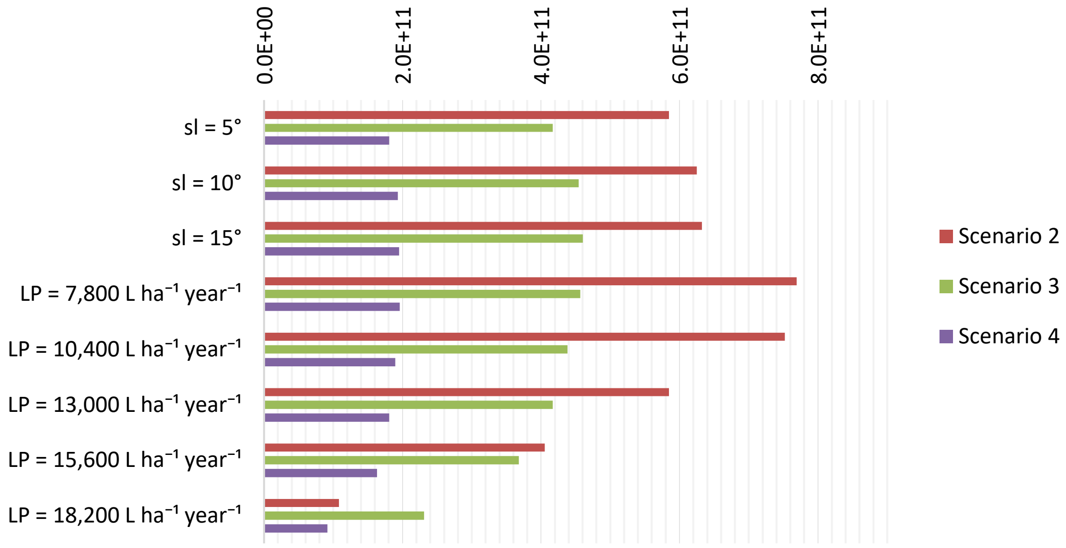


Figure S7. Sensitivity analyses on potential biodiesel production (L ha^{-1} year^{-1}) for Scenarios 2, 3 and 4 considering top suitable lands (suitability values ≥ 0.7). Scenario 2: use of fresh, brackish or salt water adjacent to known industrial CO_2 sources. Scenario 3: use of seawater without taking into account known industrial CO_2 sources. Scenario 4: use of seawater adjacent to known industrial CO_2 sources. The slope (sl) was increased from a membership midpoint of 5° to 10° and 15°. Lipid productivity (LP) was both increased and decreased by 20% and 40% from a midpoint of 13,000 L ha^{-1} year^{-1}.

4. Threatened vertebrates with more than 20% of their distribution range overlapping top suitable microalgal production lands for Scenarios 2, 3, and 4

Within top suitable microalgal production lands for Scenarios 2, 3, and 4 several threatened vertebrates would face competition with microalgal production in more than 20% of their distribution range. They correspond to the amphibian *Eupsophus queulensis*, a recently discovered and vulnerable species with a small distribution range (i.e., 12 km^2) in Central Chile; the Lima leaf-toed gecko, a critically endangered reptile restricted to an area of 393.5 km^2 in some localities around Lima, Peru; the Syrian hamster, a vulnerable rodent found in Syria and Turkey; the Atacama toad, a vulnerable amphibian found in the Chilean Atacama desert; the four-toed jerboa, a vulnerable rodent found in salt marshes and coastal deserts in Libya and Egypt; and the Peruvian plantcutter and rufous flycatcher, two vulnerable bird species found in the dry shrublands along the coastal region of Peru and Ecuador (Table S3).

Table S3. Threatened vertebrates (amphibians, birds, mammals, and reptiles) with more than 20% of their distribution ranges overlapping top suitable microalgal production lands (suitability values ≥ 0.7) for Scenarios 2, 3, and 4. IUCN Category (Cat.): Vulnerable (VU), endangered (EN), and critically endangered (CR). Total distribution range (DR), overlapping area (OA).

Microalgal cultivation	Group	Scientific name	Common name	IUCN Cat.	Location	DR (km^2)	OA (%)
Scenario 2	Mammals	*Mesocricetus auratus*	Syrian hamster	VU	Syria, Turkey	4,713.6	21.1
	Reptiles	*Phyllodactylus sentosus*	Lima leaf-toed gecko	CR	Peru	393.5	51.3
Scenario 3	Amphibians	*Eupsophus queulensis*	-	VU	Chile	12.0	87.0
		Rhinella atacamensis	Atacama toad	VU	Chile	13,654.1	21.0
	Birds	*Myiarchus semirufus*	Rufous flycatcher	VU	Peru, Ecuador	47,432.6	21.5
		Phytotoma raimondii	Peruvian plantcutter	VU	Peru, Ecuador	17,729.5	21.4
	Mammals	*Allactaga tetradactyla*	Four-toed jerboa	VU	Libya, Egypt	23,162.2	24.2
	Reptiles	*Phyllodactylus sentosus*	Lima leaf-toed gecko	CR	Peru	393.5	51.3
Scenario 4	Reptiles	*Phyllodactylus sentosus*	Lima leaf-toed gecko	CR	Peru	393.5	51.3

5. Development of optimization model based on weights and targets in energy demands

Using integer linear programming (Beyer et al. 2016) and the packages “slam” (Hornik et al. 2016) and “gurobi” (Gurobi Optimization Inc. 2017) in the software R 3.4.2, an optimization model based on targets in energy demands was developed for maximizing profitability while minimizing direct competition with agricultural lands and biodiverse areas:

$$\text{maximize} \sum_i P_i^2\, x_i / \left(\text{maximum}(A_i, B_i) + 1\right)$$

subject to

$$\sum_i D_i\, x_i = T$$

$$0 \leq x_i \leq 0.8$$

Where i corresponds to each pixel, P corresponds to microalgal profitability (ranging from 0 to 1), x corresponds to the decision variable given by the software (ranging from 0 to 0.8 and representing the available area for placing microalgal ponds), “maximum” corresponds to the maximum value among agricultural value A (ranging from 0 to 1) and biodiversity value B (ranging from 0 to 1), D corresponds to productivity values in units of energy (GJ pixel^{-1} year^{-1}), and T represents the targets in energy demands globally in 2016, 2030, and 2040 (GJ year^{-1}) based on the IEA (2017) energy production estimates (i.e., Current Policies Scenario, New Policies Scenario and Sustainable Development Scenario).

The proportion of available areas for microalgal cultivation per pixel (i.e., values ranging from 0 to 0.8) was considered after excluding water bodies (Lehner and Döll 2004), protected areas (UNEP-WCMC 2016), Key Biodiversity Areas (KBA) (BirdLife International 2016), and urban areas (Schneider et al. 2009). It was assumed that 80% of the area within each pixel can be utilized for microalgal cultivation, with a remaining 20% for associated infrastructure (Wigmosta et al. 2011).

Agriculture values were transformed using a linear function with a maximum of USD 800 ha^{-1}, as beyond this value lands are considered highly profitable (Naidoo and Iwamura 2007). Biodiversity value resulted from overlaying the number of vertebrate species, the number of threatened vertebrates species (Jenkins et al. 2013), the presence of islands, and the presence of areas with low human pressures (Venter et al. 2016) using the OR Boolean operator. For the number of vertebrate species and the number of threatened vertebrate species linear functions were applied; while for the presence of islands and areas with low human pressures sigmoid functions were applied (i.e., a small membership function with a membership midpoint of 1,000,000 km^2 for islands and a small membership function with a midpoint of 4 for areas with low human pressures), resulting in most islands and areas with none and low human pressures (Venter et al. 2016) as important for biodiversity conservation.

We investigated alternative solutions in which the agricultural and biodiversity values were not taken into account, based on a matrix of weights (Table S4), and in which targets in microalgal biodiesel production increased from 10% to 40% based on 2016’s transport energy demands.

Table S4. Matrix of weights assigned to assess the influence of agricultural (A) and biodiversity value (B) in the optimization model.

Weight A	**Weight B**
1	1
1	0
0	1
0	0

Chapter 3. Contribution to the authorship

I was in charge of the conception and design of the project; acquisition, analysis, and interpretation of the research data; drafting, analysis, and critical writing of the manuscript.

CHAPTER 3. Best areas for microalgal biofuel production at national scales: Conflicts with agricultural lands and biodiversity

Diego F. Correa[1, 2*], Hawthorne L. Beyer[2], Hugh P. Possingham[2,3], Joseph E. Fargione[4], Jason D. Hill[5], Peer M. Schenk[1]

[1]Algae Biotechnology Laboratory, School of Agriculture and Food Sciences, The University of Queensland, Brisbane, QLD 4072, Australia

[2] Centre for Biodiversity and Conservation Science CBCS, The University of Queensland, Brisbane, QLD 4072, Australia

[3] The Nature Conservancy, Arlington, VA 22203, USA

[4] The Nature Conservancy, Minneapolis, MN 55415, USA

[5] Department of Bioproducts and Biosystems Engineering, The University of Minnesota, St. Paul, MN 55108, USA

ABSTRACT

While several biofuel production systems based on non-food crops have been explored as alternatives for replacing first generation biofuels, their potential impacts on food production and biodiversity remain unclear. Microalgal production systems can produce higher levels of biofuels per unit area compared to food crops, and do not depend on fertile soils or freshwater; however, little is known about potential conflicts of large-scale microalgal production with agricultural areas and biodiversity for fulfilling domestic energy targets. Using a GIS-based multiple-criteria decision analysis (MCDA) and integer linear programming we selected the most cost-effective areas for large-scale microalgal production (i.e., where water, flat lands, and transport networks are available, and where high lipid productivities can be achieved), able to satisfy 30% of each country's transport energy demands in 2016 and 2050 while avoiding areas of high agricultural and biodiversity value. Main areas for microalgal biofuel production mainly corresponded drier low-latitude areas or drier lowlands within countries. In around one-quarter of the countries, mainly located in the Middle East, North Africa, and non-OECD Americas, microalgal production could currently overlap with areas of median potential agricultural revenues lower than 225 USD ha^{-1}, and median biodiversity values lower than 260 and 16 vertebrate species and threatened vertebrate species, respectively. While domestic biofuel production could help to fulfill national energy targets and reduce the external dependence on energy, scaling-up microalgal production farms in countries with either high energy demands or without available human-transformed dry lands could cause significant conflicts with food production and biodiversity.

Keywords: Microalgae, biofuels, agriculture, biodiversity, sustainability, transport, fossil fuel

1. INTRODUCTION

Current energy production systems, based in the use of fossil fuels, are the primary source of anthropogenic greenhouse gas emissions (Hartmann et al. 2013), contributing to global warming (Cox et al. 2000, Rockström et al. 2009) and its impacts on ecosystems (Bellard et al. 2012), society, and economy (Ciscar et al. 2011). Replacing fossil fuels by renewable energy sources has been proposed as the main mechanism for reducing CO_2 emissions (Jacobson and Delucchi 2011) and limiting global warming to well below 2°C (IPCC 2015) along with its undesired environmental end socioeconomic consequences (UN 2015). In the face of future higher energy demands (EIA 2016, IEA 2017), countries have become increasingly interested in ensuring a domestic production of renewable energy so as to reduce uncertainties associated to global energy markets (Correlje and Van der Linde 2006, Baumann 2008) and to replace unsustainable energy sources (Asif and Muneer 2007, da Silva et al. 2016, Kumar 2016). This can lead to a different set of environmental impacts compared to fossil fuels (Akella et al. 2009, Berrill et al. 2016), including land-use changes within areas suitable for agricultural production (Owusu and Asumadu-Sarkodie 2016) or with high biodiversity value (Gasparatos et al. 2017).

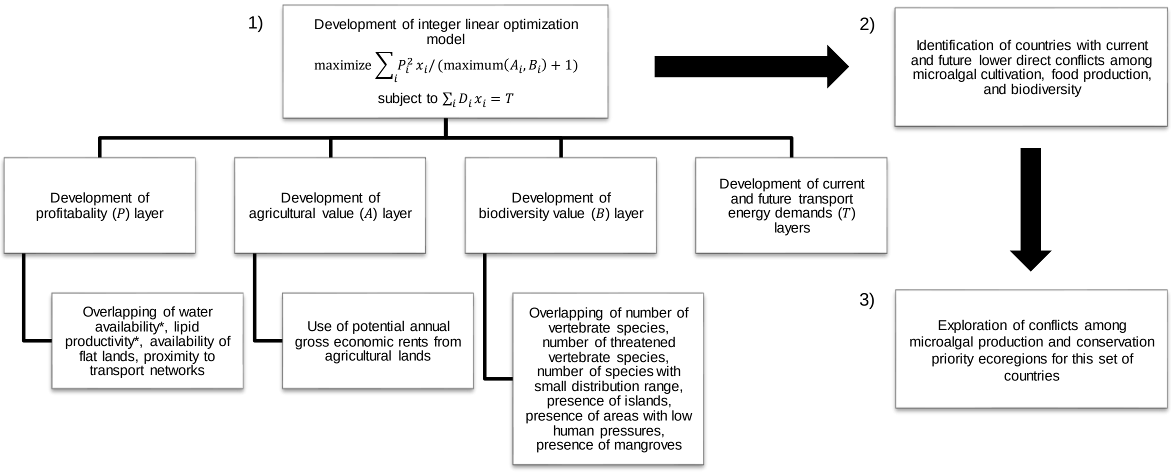
Biofuel production, based on the transformation of biomass into carbon-rich energy carriers aimed at replacing fossil fuels (e.g., gasoline by bioethanol and diesel by biodiesel) (Naik et al. 2010), could quadruple by 2040 compared to 2016 (i.e., from 1.7 to 8.1 million barrels of oil equivalent day^{-1}) despite an increased share of transportation driven by electricity (IEA 2017). This is because biofuels are expected to remain a prime source of energy for ships, planes, and long-haul trucks (Fulton et al. 2015). However, current first generation biofuel production systems (i.e., those derived from food crops) compete with agricultural lands and thus displace food production (Lambin and Meyfroidt 2011), leading to the direct and indirect transformation of biodiverse (Fargione et al. 2010, Immerzeel et al. 2014, Correa et al. 2017, Elshout et al. 2019) and carbon-rich systems into monocultures (Fargione et al. 2008). A future expansion of first generation biofuels would drive further land-use changes within and outside agricultural lands, potentially impairing food security particularly in developing economies (Naylor et al. 2007, To and Grafton 2015) while driving the transformation and degradation of native ecosystems (Butler and Laurance 2009, Wich et al. 2014, Searchinger et al. 2015).

Microalgal biofuel production systems, which have been proposed as a promising alternative to first generation biofuels, offer higher biofuel productivities per unit area and do not depend on arable lands or freshwater resources for their cultivation (Chisti 2007, Schenk et al. 2008, Correa et al. 2017). As a consequence, compared to first generation biofuels, microalgal production systems could offer land savings and their cultivation could more easily be constrained to areas unsuitable for agriculture and with low biodiversity values (Correa et al. 2019). Furthermore, they offer great potential for water remediation (i.e., recycling nutrients from wastewater sources) (Abdel-Raouf et al. 2012) and for CO_2 mitigation (i.e., re-using CO_2 produced by industries) (Wang et al. 2008). Provided there are reductions in their production costs—achievable through the development of biorefinery systems that increase the profitability of biofuels based on the production of high-value products (e.g., food, animal feed) (Zhu 2015, Ruiz et al. 2016), coupled with the cultivation of highly productive microalgal strains (Chisti 2008, Ajjawi et al. 2017), the development of more cost-effective cultivation technologies (e.g., mixotrophic cultivation systems) (Roostaei et al. 2018) that reduce energy inputs and enhance nutrient recycling (e.g., through anaerobic digestion) (González-González et al. 2018), and the co-location with free nutrient and CO_2 sources (e.g., from wastewater and industries) (Slade and Bauen 2013, Acién et al. 2018)—microalgal biofuels could complement or eventually replace other biofuel production alternatives (Chisti 2008, Schenk et al. 2008, Correa et al. 2019). However, if production is concentrated within countries for fulfilling domestic energy targets, potential conflicts with agricultural lands or biodiversity could occur.

Under future increases in food demands, projected in around 60% between 2006 and 2050 (Alexandratos and Bruinsma 2012) and higher targets for ensuring biodiversity conservation and the services that ecosystem provide (UN 2015), understanding the potential conflicts between microalgal biofuel production, agricultural value, and biodiversity, can guide decision making towards the identification of more sustainable biofuel production alternatives (Correa et al. 2019). Aiming at reducing uncertainties in global energy markets and transport costs (Baumann 2008), we provide best areas for fulfilling each country's 30% current and future domestic transport energy demands through microalgal biofuels, while decreasing direct competition with lands of high agricultural and biodiversity value within countries. Furthermore, we 1) Identify countries where current and future high lipid productivity levels and minimal overlap among microalgal production, agricultural value, and biodiversity value would occur, and 2) Explore potential conflicts among microalgal production and areas of high ecological importance (i.e., biodiverse areas and conservation priority ecoregions) for this set of countries.

2. METHODS

We aimed at selecting suitable areas for fulfilling each country's 30% current and future domestic transport energy demands through microalgal biofuels, while decreasing direct competition with lands of high agricultural and biodiversity value (Fig. 1). Furthermore, we identified countries where minimal overlap among microalgal production, agricultural value, and biodiversity value would occur; and explored potential conflicts among microalgal production and conservation priority ecoregions for this set of countries.



x

*Figure 1. Diagram showing the main steps involved to: 1) Develop an integer linear optimization model to select best areas for fulfilling each country's 30% current and future domestic transport energy demands through microalgal biofuels while decreasing direct competition with lands of high agricultural and biodiversity value, 2) Identify countries with lower direct conflicts among microalgal production, food production, and biodiversity, and 3) Explore conflicts with conservation priority ecoregions for this set of countries. *Estimations on future aridity index and future microalgal lipid productivity were developed considering changes in precipitation, potential evapotranspiration, and temperature, based on an ensemble model for the Representative Concentration Pathway (RCP) 8.5 (See Supplementary Information for details).*

2.1 Development of integer linear programming model

Based on integer linear programming (Beyer et al. 2016) a model was developed to select potential microalgal production areas with high profitabilities and low direct competition with food production and biodiversity, for fulfilling each country's 30% of transport energy demands in 2016 and 2050 based on two microalgal cultivation scenarios: Scenario 1 (i.e., use of fresh/brackish/salt water) and

Scenario 2 (i.e., use of seawater). We used the software R and Gurobi optimizer for resolving the following equation (Correa et al. 2019):

$$\text{maximize} \sum_i P_i^2 \, x_i / \, (\text{maximum}(A_i, B_i) + 1)$$

subject to

$$\sum_i D_i \, x_i = T$$

$$0 \leq x_i \leq 0.8$$

Where i corresponds to each pixel, P corresponds to the microalgal profitability layer (ranging from 0 to 1), x corresponds to the decision variable given by the software (ranging from 0 to 0.8, assuming that 20% of each pixel would be used for operational infrastructure) (Wigmosta et al. 2011), "maximum" corresponds to the maximum value among agricultural value A (ranging from 0 to 1) and biodiversity value B (ranging from 0 to 1), D corresponds to productivity values in units of energy (GJ pixel^{-1} year^{-1}), and T represents 30% of each country's transport energy demands for 2016 and 2050 (GJ year^{-1}). The squaring of the profitability as the numerator and the maximum value among A or B as the denominator, ensures that pixels with lower or average profitabilities, and with either high agricultural or high biodiversity values, are not part of final solutions. The percentage of available area for microalgal cultivation was determined per pixel after excluding water bodies larger than 100 km^2 (Lehner and Döll 2004), protected areas (UNEP-WCMC 2016), Key Biodiversity Areas (KBA) (BirdLife International 2016), and urban areas (i.e., built environments) (Schneider et al. 2009).

Lands covers potentially replaced by microalgal production (i.e., considering cultivation areas plus associated infrastructure) were identified based on the MODIS-derived global mosaic for 2012 at a resolution of 5 arcminutes (Channan et al. 2014) for each cultivation scenario.

2.2 Development of layers (microalgal profitability, agricultural value, and biodiversity value)

The profitability layer was obtained through a GIS-based multiple-criteria decision analysis (MCDA) developed in the software ArcGIS 10.5 at a spatial resolution of 5 × 5 km (see Supplementary Information for details). The profitability layer resulted from overlaying water availability, microalgal lipid productivity, availability of flat lands, and proximity to main transport networks (i.e., main roads and railroads), which are necessary for microalgal cultivation (i.e., water availability) and for decreasing costs in microalgal biofuel production (i.e., lipid productivity, flat lands, proximity to transport networks) (Chisti 2007, Schenk et al. 2008, Lundquist et al. 2010, Wigmosta et al. 2011, Slade and Bauen 2013, Venteris et al. 2014, Slegers et al. 2015). For Scenario 1 water availability included water from rivers, irrigation dams, or fresh/brackish/salt groundwater sources after accounting for water depletion (Brauman et al. 2016), as well as water from precipitation (i.e., aridity index) and seawater. For Scenario 2, the water source corresponded to seawater (i.e., excluding inland brackish/salt water bodies such as the Aral and the Caspian seas). Our model did not constrain siting based on the location of CO_2 sources (e.g., CO_2 from industries, anaerobic digesters, fermenters in biorefineries) or free nutrient sources (e.g., wastewater treatment facilities), which, in spite of reducing biofuel production costs (Lundquist et al. 2010, Slade and Bauen 2013, Venteris et al. 2014) are not consistently mapped globally and would further limit the amount of suitable lands for microalgal biofuel production (Correa et al. 2019).

For determining the future siting of microalgal production farms, which could result from changes in the aridity index (i.e., based on changes in precipitation, potential evapotranspiration, and temperature), and changes in lipid productivities (i.e., based on changes in temperature) (See Supplementary Information for details), we developed ensemble models based on several climate change scenarios. For each Representative Concentration Pathway (RCP) (i.e., 2.6, 4.6, 6.0, and 8.5) we constructed an ensemble model by averaging mean monthly temperatures, minimum monthly temperatures, maximum monthly temperatures, and mean annual precipitation values among the following General Circulation Models (GCMs): BCC-CSM1-1, CCSM4, GISS-E2-R, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM-CHEM, MRI-CGCM3, and NorESM1-M (Hijmans et al. 2005). The high emissions RCP 8.5 (Riahi et al. 2011) was used to find potential microalgal production areas with high profitabilities and low direct competition with food production and biodiversity by 2050.

Agricultural value corresponded to the potential annual gross economic rents from agricultural lands (Naidoo and Iwamura 2007). Biodiversity value resulted from overlaying the number of vertebrate species, the number of threatened vertebrate species, the number of vertebrate species with small distribution ranges (i.e., considering amphibians, birds, and mammals) (Jenkins et al. 2013), the presence of islands (which compared to the mainland harbour more endemic species and populations) (Kier et al. 2009, Tershy et al. 2015, McCreless et al. 2016), the presence of areas with low human pressures on the environment (i.e., based on the Global Human Footprint) (Venter et al. 2016), and the presence of mangroves (which hold key ecological significance and provide a wide range of ecosystem services) (Giri et al. 2011).

2.3 Calculation of current and future transport energy demands

Countries corresponded to sovereign states and administrative units with an associated ISO based on the GADM database v.2. Transport energy demands in 2016 were obtained for each country in million tonnes of oil equivalent (MTOE) (IEA 2018). These values were transformed into GJ by multiplying by the conversion factor 4.1868×10^{7} GJ $MTOE^{-1}$ (IEA 2017). For countries without information—i.e., other Africa, other non-OECD Asia, and other non-OECD Americas (IEA 2018)—transport energy demands were assumed proportional to their population (UN 2017). Each country’s future transport energy demands were estimated based on the annual growth on transport energy consumption between 2012 and 2040 per economic region (Africa, non-OECD Asia, non-OECD Americas, the Middle East, non-OECD Europe and Eurasia, OECD Europe) and selected countries (Australia, Brazil, Canada, Chile, China, Japan, India, Mexico, New Zealand, South Korea, and the USA) (EIA 2016) (Table S3, Supplementary Information).

2.4 Identification of countries with current and future lower direct conflicts with food production and biodiversity

Based on median values for lipid productivity, agricultural value, and biodiversity value globally, countries that offer high microalgal productivities (i.e., lipid productivity values higher than the global median value) at lower direct conflicts with high-value agricultural lands and biodiversity (i.e., agricultural and biodiversity values lower than the global median values), were identified for 2016 and 2050. For these set of countries, lands covers potentially replaced by microalgal production (i.e., considering cultivation areas plus associated infrastructure) were identified based on the MODIS-derived global mosaic for 2012 at a resolution of 5 arcminutes (Channan et al. 2014). Furthermore, the potential overlap among microalgal production areas and the Global 200 ecoregions, which have been identified key for biodiversity conservation globally (Olson and Dinerstein 2002), was determined.

3. RESULTS

3.1 Best areas for siting microalgal biofuel production farms at national scales

Globally, between 1,010.5 thousand km^2 and 1,016.8 thousand km^2 would be needed to fulfill 30% of each country's transport energy demands in 2016, based on Scenario 1 (i.e., use of fresh, brackish or salt water) and 2 (i.e., use of seawater), respectively (Table 1). 70% of microalgal production areas would fall within OECD countries in the Americas (i.e., USA, Canada, Mexico), Europe (i.e., Germany, United Kingdom, France, Italy), and Asia (i.e., Japan and South Korea), as well as non-OECD countries like China, Russia, India, and Brazil (Fig. 2). For Scenario 1, 80% of microalgal production areas would overlap mixed forests, croplands, grasslands, cropland/natural vegetation mosaics, woody savannas, barren or sparsely vegetated lands, and open shrublands (i.e., 17%, 15%, 14%, 12%, 9%, 7%, and 6% of total microalgal production land, respectively). For Scenario 2, 80% of microalgal production areas would overlap mixed forests, croplands, cropland/natural vegetation mosaics, woody savannas, barren or sparsely vegetates lands, open shrublands, evergreen broadleaf forests, and grasslands (i.e., 19%, 17%, 14%, 11%, 6%, 5%, 5%, and 4% of total microalgal production land, respectively) (Fig. 3, Table 1).

Around half of the analyzed countries could meet 30% transport energy demands in 2016 by microalgal production in lands with median agricultural values lower than 0.19 and 0.28, based on Scenarios 1 and 2, respectively. In these lands, mainly located within temperate areas in the Northern Hemisphere (i.e., median latitudes of 38°N both for Scenarios 1 and 2), median potential agricultural revenues would be between 75–108.5 USD ha^{-1} (Naidoo and Iwamura 2007) for Scenarios 1 and 2, respectively. Similarly, around half of the analyzed countries could meet 30% of current transport energy demands in lands with median biodiversity values lower than 0.28, both for Scenarios 1 and 2. In these lands, the median number of vertebrate and threatened vertebrate species is (i.e., based on amphibians, birds, and mammals) would be between 212–213 vertebrate species and between 3–4 threatened vertebrate species for Scenarios 1 and 2, respectively.

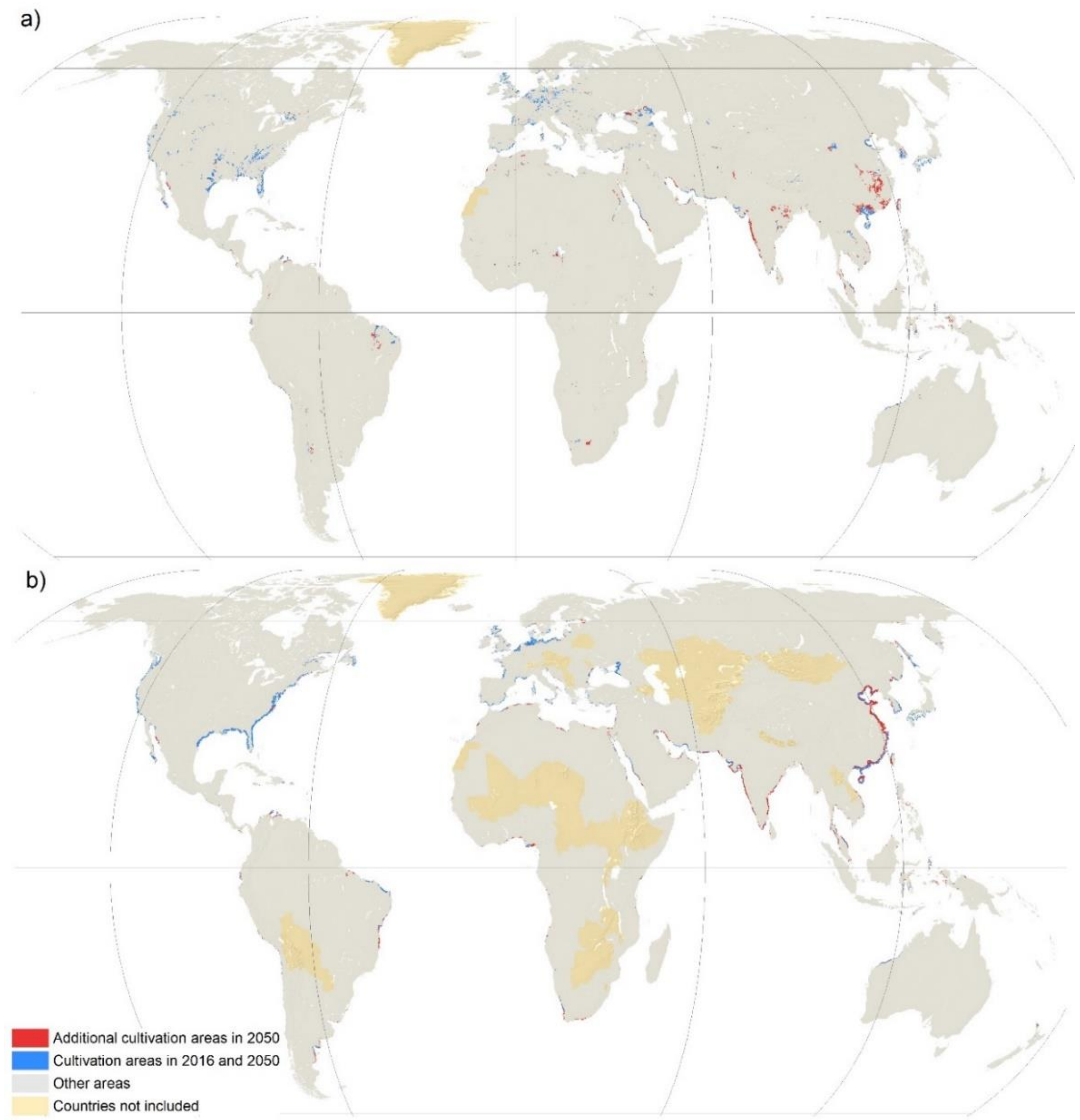


Figure 2. Cultivation areas for fulfilling each country's 30% of transport energy demands in 2016 and 2050 by microalgal production for a) Scenario 1 (use of fresh, brackish and saltwater sources) and b) Scenario 2 (use of seawater). These areas are based on an optimization model that maximizes microalgal profitability and minimizes direct competition with high-value agricultural lands and biodiverse areas.

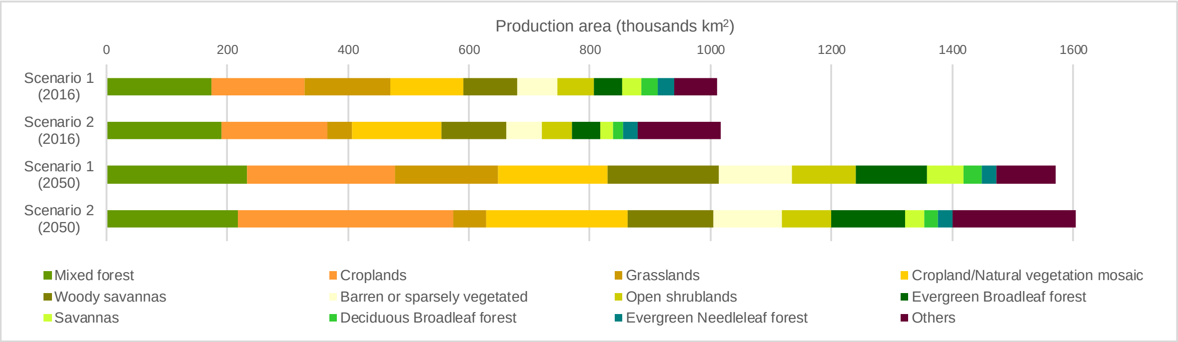


Figure 3. Land-cover composition of areas that fulfill each country's 30% transport energy demands in 2016 and 2050, considering Scenarios 1 (i.e., use of fresh, brackish, and salt water) and 2 (i.e., use of seawater). Land covers are based on the MODIS derived global mosaic for 2012 at a resolution of 5 arcminutes (Channan et al. 2014).

Table 1. Land-cover composition within areas that fulfill each country's 30% transport energy demands in 2016 and 2050, based on Scenarios 1 (i.e., use of fresh, brackish, and salt water) and 2 (i.e., use of seawater). Land covers are based on the MODIS derived global mosaic for 2012 at a resolution of 5 arcminutes (Channan et al. 2014). Land areas are shown in thousands km^2. The relative changes (Rel.) in areas between 2016 and 2050 are shown for each land cover.

Land Cover	**Scenario 1 (2016)**		**Scenario 2 (2016)**		**Scenario 1 (2050)**			**Scenario 2 (2050)**		
	Area	**%**	**Area**	**%**	**Area**	**%**	**Rel. (%)**	**Area**	**%**	**Rel. (%)**
Mixed forest	174.1	17	190.6	19	233.0	15	34	218.4	14	15
Croplands	153.3	15	175.8	17	244.7	16	60	355.1	22	102
Grasslands	141.9	14	40.6	4	170.5	11	20	54.4	3	34
Cropland/Natural vegetation mosaic	120.9	12	147.3	14	182.0	12	51	234.2	15	59
Woody savannas	90.2	9	106.9	11	184.2	12	104	142.0	9	33
Barren or sparsely vegetated	66.2	7	59.6	6	119.6	8	81	113.3	7	90
Open shrublands	59.5	6	50.2	5	106.8	7	79	83.0	5	66
Evergreen Broadleaf forest	47.4	5	46.0	5	117.5	7	148	122.1	8	166
Savannas	32.3	3	21.5	2	60.8	4	88	31.9	2	48
Deciduous Broadleaf forest	27.1	3	17.3	2	29.6	2	9	21.4	1	24
Evergreen Needleleaf forest	26.9	3	23.3	2	24.4	2	-9	25.4	2	9
Others	70.8	7	137.8	14	98.4	6	39	203.0	13	47
Total	1,010.5	100	1,016.8	100	1,571.4	100	56	1,604.3	100	58

In around one-quarter of countries, mainly located in Africa, the Middle East, non-OECD Americas, and non-OECD Asia and Oceania, 30% of transport energy demands could be fulfilled by achieving high microalgal productivities (i.e., median lipid productivity values higher than 20.3 and 20.2 m^3 ha^{-1} year^{-1} for Scenarios 1 and 2, respectively) at lower direct competition with food production or biodiversity (i.e., median agricultural values lower than 0.19 and 0.28 for Scenarios 1 and 2, respectively, and median biodiversity values lower than 0.28 for both Scenarios 1 and 2) (Fig. 4, Tables S4, S5, S6, and S7 in Supplementary Information). Within these countries, microalgal production would mainly overlap with barren or sparsely vegetated lands and open shrublands for the different cultivation scenarios (i.e., ranging from 88 to 92% of total microalgal production area) (Table 2). Between 30% and 35%, and between 46% and 53% of microalgal production areas for Scenarios 1 and 2, respectively, would overlap ecoregions of high conservation priority (Olson and Dinerstein 2002), mostly on arid and semi-arid lands (i.e., between 94% and 97%, and between 74% and 96% of overlapping ecoregions for Scenarios 1 and 2, respectively) (Table S8 in Supplementary Information). Microalgal cultivation would overlap less than 5% of each of these ecoregions (Table 3).

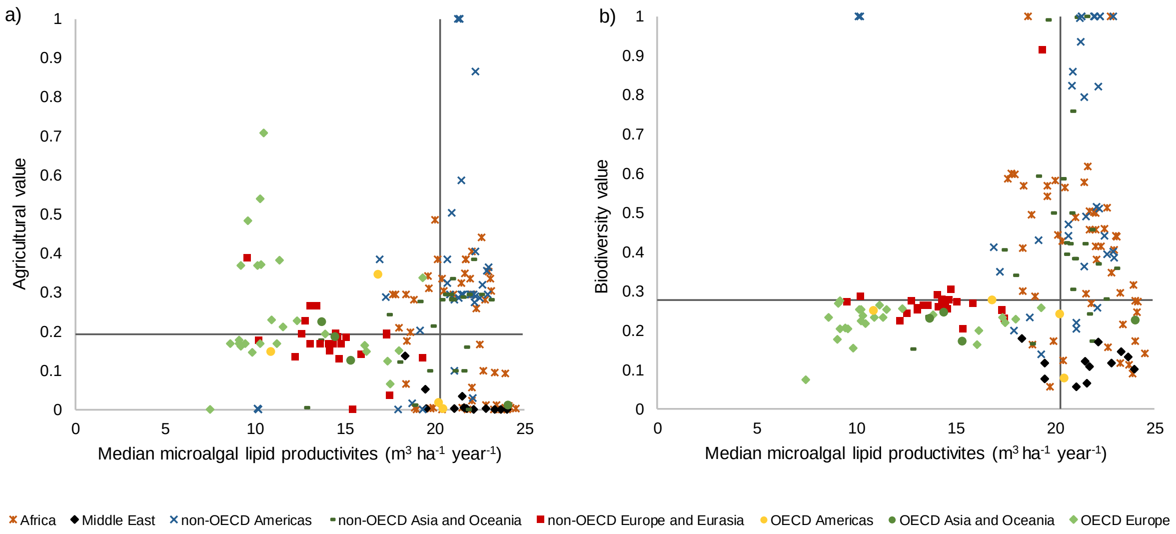


Figure 4. Median microalgal lipid productivities and a) agricultural value of lands or b) biodiversity value of lands that satisfy each country's 30% transport energy demands in 2016, based on Scenario 1 (use of fresh, brackish, and saltwater sources). The quadrants are delimited by the median productivity, agricultural, and biodiversity values globally.

Table 2. Land-cover composition within areas that fulfill each country's 30% transport energy demands in 2016 and 2050, considering countries where high microalgal productivities (HP) can be achieved at lower competition with agriculture (LA) and biodiversity (LB). Median microalgal lipid productivity > 20.3, 20.2, 20.1, and 19.9 m^3 ha^{-1} year^{-1} for Scenario 1 in 2016, Scenario 2 in 2016, Scenario 1 in 2050, and Scenario 2 in 2050, respectively. Median agricultural values < 0.19, 0.28, 0.22, and 0.28 for Scenario 1 in 2016, Scenario 2 in 2016, Scenario 1 in 2050, and Scenario 2 in 2050, respectively. Median biodiversity values < 0.28, 0.28, 0.28, and 0.31 for Scenario 1 in 2016, Scenario 2 in 2016, Scenario 1 in 2050, and Scenario 2 in 2050, respectively. Land covers are based on the MODIS derived global mosaic for 2012 at a resolution of 5 arcminutes (Channan et al. 2014). Land areas are shown in thousands of km^2. The relative changes in land areas between 2016 and 2050 are shown for each land cover.

Land Cover	**Scen. 1 HP-LA**		**Scen. 1 HP-LB**		**Scen. 2 HP-LA**		**Scen. 2 HP-LB**		**Scen. 1 HP-LA**	**Scen. 1 HP-LB**	**Scen. 2 HP-LA**	**Scen. 2 HP-LB**
	Area	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Relative change 2016–2050 (%)**			
Barren or sparsely vegetated	50.5	68.1	49.7	78.1	48.2	60.1	48.2	63.5	73.8	75.9	92.7	92.7
Open shrublands	15.8	21.4	8.7	13.6	22.0	27.5	20.9	27.5	234.8	464.4	63.2	66.3
Grasslands	1.5	2.0	0.1	0.2	1.4	1.8	0.2	0.2	14.1	881.8	93.2	174.3
Cropland/Natural vegetation mosaic	0.8	1.1	0.4	0.6	1.1	1.4	0.3	0.4	-18.0	217.7	647.8	285.5
Savannas	0.5	0.7	0.2	0.3	0.1	0.2	0.1	0.2	143.1	119.1	2,244.4	214.9
Evergreen Broadleaf forest	0.3	0.4	0.3	0.5	0.6	0.7	0.3	0.4	97.9	132.0	4,386.3	150.5
Woody savannas	0.1	0.1	0.2	0.2	0.1	0.1	0.2	0.3	489.2	353.1	404.2	124.1
Croplands	0.1	0.1	0.3	0.4	0.1	0.1	0.3	0.4	6,446.9	1,767.7	981.1	224.6
Closed shrublands	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-	-	138.4	138.4
Others	4.4	6.0	3.8	6.0	6.5	8.0	5.4	7.1	130.0	174.7	201.1	125.2
Total	74.1	100.0	63.6	100.0	80.2	100.0	75.9	100.0	116.8	145.6	138.4	89.9

Table 3. Percentage of arid/semiarid priority ecoregions for global conservation (Olson and Dinerstein 2002) overlapping microalgal production areas that fulfill each country's 30% transport energy demands in 2016 and 2050. Countries where higher microalgal productivities (HP) can be achieved at lower competition with agriculture (LA) and biodiversity (LB) are considered for Scenarios 1 (i.e., use of fresh, brackish and salt water) and 2 (i.e., use of seawater). Land areas are shown in km^2.

Ecoregion	**2016**				**2050**			
	Scen. 1 HP-LA	**Scen. 1 HP-LB**	**Scen. 2 HP-LA**	**Scen. 2 HP-LB**	**Scen. 1 HP-LA**	**Scen. 1 HP-LB**	**Scen. 2 HP-LA**	**Scen. 2 HP-LB**
Arabian Highlands Woodlands and Shrublands	1.3	1.3	0.9	1.4	3.2	3.2	3.3	3.3
Atacama-Sechura Deserts	0.7	0.7	0.8	0.7	1.0	1.0	1.0	1.0
Carnavon Xeric Shrubs	2.1	2.1	1.2	2.4	2.8	2.8	3.6	3.6
Chilean Matorral	0.3	0.3	0.2	0.3	0.6	0.6	0.6	0.6
Great Sandy-Tanami-Central Ranges Desert	0.0	0.0	0.0	-	0.0	0.0	0.0	0.0
Horn of Africa Acacia Savannas	0.1	-	-	-	0.3	-	-	-
Madagascar Spiny Thicket	-	-	0.1	0.1	-	-	0.1	0.1
Mediterranean Forests, Woodlands and Scrub	0.1	0.1	-	-	-	-	0.0	0.0
Namib-Karoo-Kaokoveld Deserts and Shrublands	0.7	0.0	-	-	1.7	1.6	-	-
Northern Australia and Trans-Fly Savannas	0.2	0.2	0.5	0.2	0.3	0.3	0.2	0.2
Rann of Kutch Flooded Grasslands	-	-	-	-	0.1	0.1	0.5	0.5
Socotra Island Desert	-	-	4.2	-	-	-	-	-
Sonoran-Baja Deserts	-	-	4.8	4.7	6.3	6.3	6.4	6.4
Southern Mexican Dry Forests	-	-	0.0	0.1	0.7	0.7	0.6	0.6
Sudd-Sahelian Flooded Grasslands and Savannas	-	-	-	-	0.0	0.0	-	-

3.2 Future siting microalgal biofuel production farms at national scales

Based on a high-emissions climate change scenario (i.e., RCP 8.5), total microalgal production area by 2050 would increase between 56% and 58% compared to 2016 to fulfill a future 30% target in transport energy demands per country (Table 1). For Scenario 1, increases in land-cover overlapping would be highest for evergreen broadleaf forests, followed by woody savannas, savannas, barren or sparsely vegetated lands, and open shrublands (i.e., 148%, 104%, 88%, 81%, and 79%, respectively). For Scenario 2, increases in land-cover overlapping would be highest for evergreen broadleaf forests, followed by croplands, barren or sparsely vegetated lands, open shrublands, and cropland/natural vegetation mosaics (i.e., 166%, 102%, 90%, 66%, and 59%, respectively).

Microalgal production areas for fulfilling 30% of each country's transport energy demands would increase by around 4-fold in India; by around three-fold in most African and non-OECD Asian and Oceanian countries and China; and by around two-fold in non-OECD American countries, Middle Eastern countries, and Chile. In contrast, the lowest increases in production areas would occur in non-OECD European and Eurasian countries and most OECD countries (i.e., Australia, Canada, Japan, Mexico, New Zealand, United states, South Korea and OECD Europe) (Fig. 5).

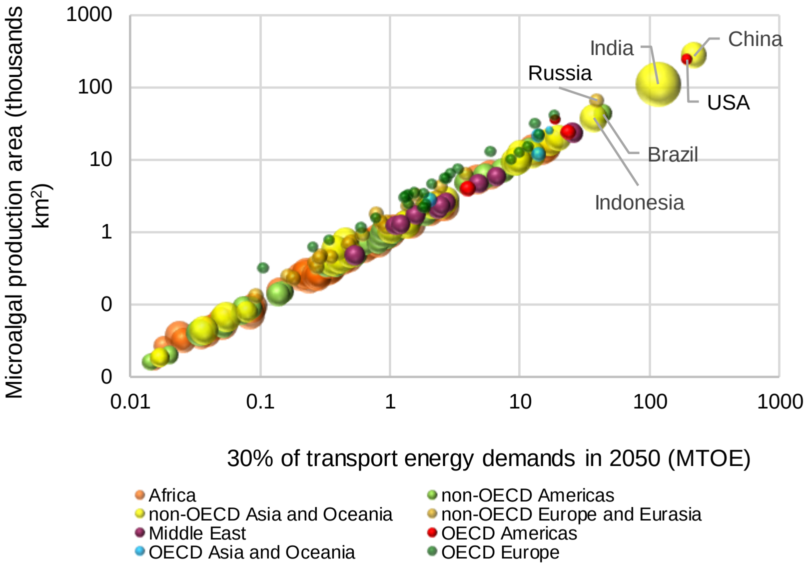


Figure 5. Microalgal production areas needed to satisfy each country's 30% transport energy demands in 2050 ($\log_{10}$ scale) under a Representative Concentration Pathway (RCP) 8.5 climate change scenario. The width of the circles is proportional to increases in microalgal production areas by 2050 compared to 2016 (i.e., ranging from 0.8 in Japan to 4.4 in India between 2016 and 2050). Million tonnes of oil equivalent (MTOE).

In around one-quarter of the countries, 30% of future transport energy could be met in lands with high productivities (i.e., median lipid productivity values higher than 20.1 and 19.9 m^3 ha^{-1} $year^{-1}$ for

Scenarios 1 and 2, respectively) at lower direct competition with food production or biodiversity (i.e., median agricultural values lower than 0.22 and 028, and median biodiversity values lower than 0.28 and 0.31, for Scenarios 1 and 2, respectively) (Figs. 6, 7, 8, and 9). As in 2016, these countries are mainly located in Africa, the Middle East, non-OECD Americas, and non-OECD Asia and Oceania, and microalgal production would mainly overlap with barren or sparsely vegetated lands and open shrublands for the different cultivation scenarios (i.e., ranging from 67 to 89% of total microalgal production area within these countries), over less than 6.4% of total land area within each high conservation priority ecoregion (Table 3).

For Scenarios 1 and 2, countries that consistently could offer high productivities at lower competition with areas of high agricultural and biodiversity (i.e., for 2016 and 2050) correspond to Australia, Chile, Djibouti, Egypt, Eritrea, Haiti, Iran, Iraq, Kuwait, Madagascar, Mauritania, Oman, Pakistan, Papua New Guinea, Qatar, Saudi Arabia, Somalia, Sudan, United Arab Emirates, and Yemen.

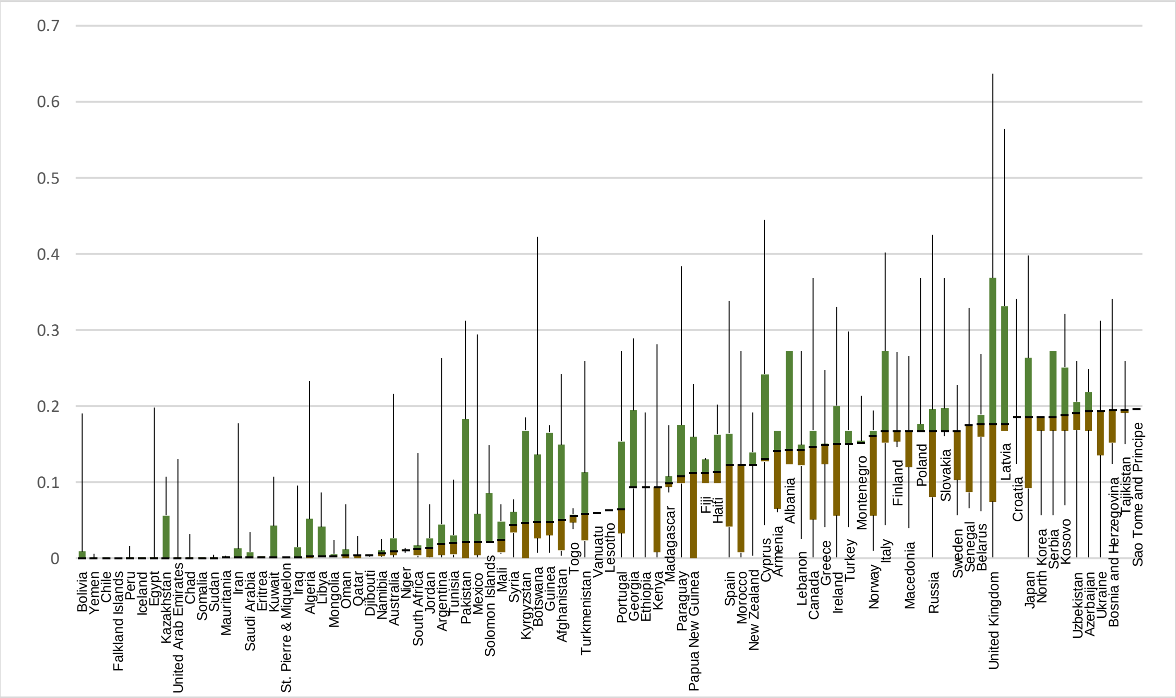


Figure 6. Boxplots for agricultural value of lands in areas that fulfill each country's 30% transport energy demands by 2050, based on Scenario 1 (use of fresh, brackish and saltwater sources). Countries with median agricultural values lower than the global median

value (i.e., median agricultural value < 0.22) are included. Maximum and minimum values within countries are shown within the whiskers.

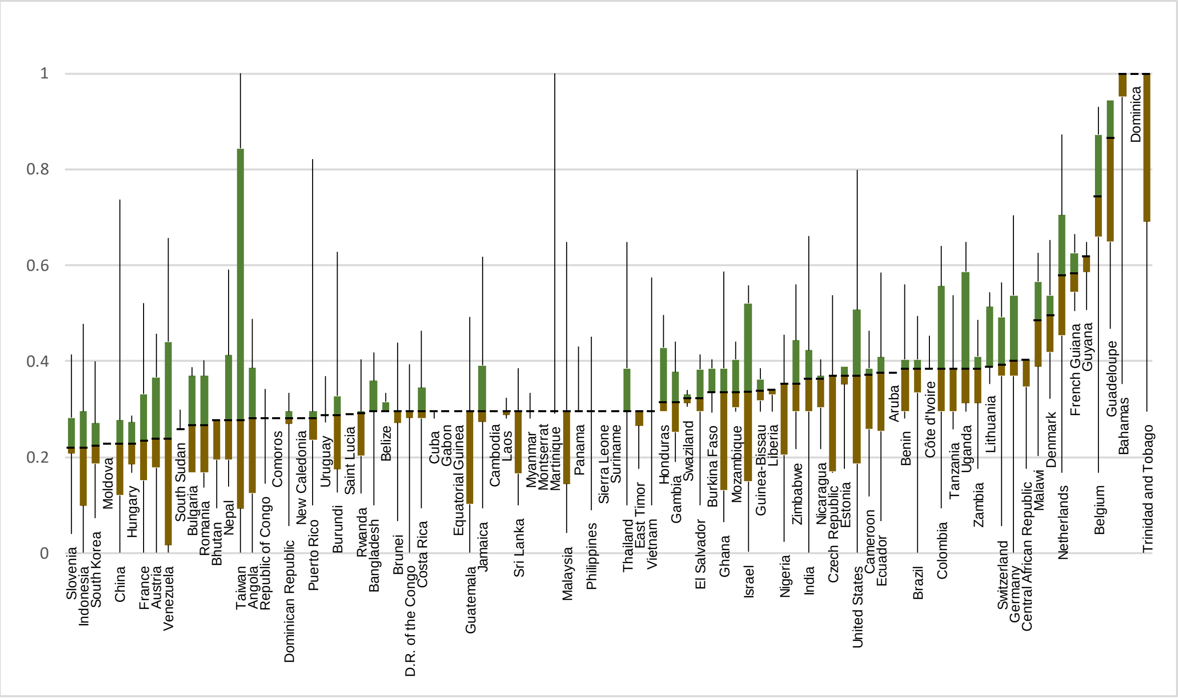


Figure 7. Boxplots for agricultural value of lands in areas that fulfill each country's 30% transport energy demands by 2050, based on Scenario 1 (use of fresh, brackish and saltwater sources). Countries with median agricultural values higher than the global median value (i.e., median agricultural value ≥ 0.22) are included. Maximum and minimum values within countries are shown within the whiskers.

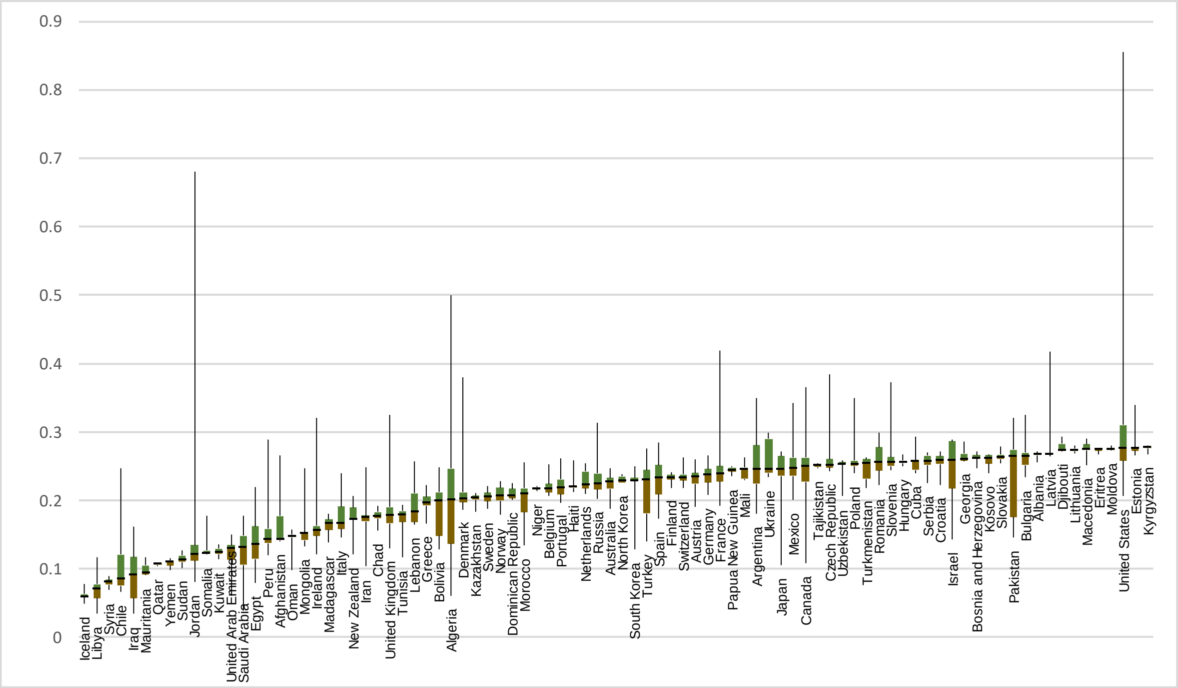


Figure 8. Boxplots for biodiversity value of lands in areas that fulfill each country's 30% transport energy demands by 2050, based on Scenario 1 (use of fresh, brackish and saltwater sources). Countries with median biodiversity values lower than the global median value (i.e., median biodiversity value < 0.28) are included. Maximum and minimum values within countries are shown within the whiskers.

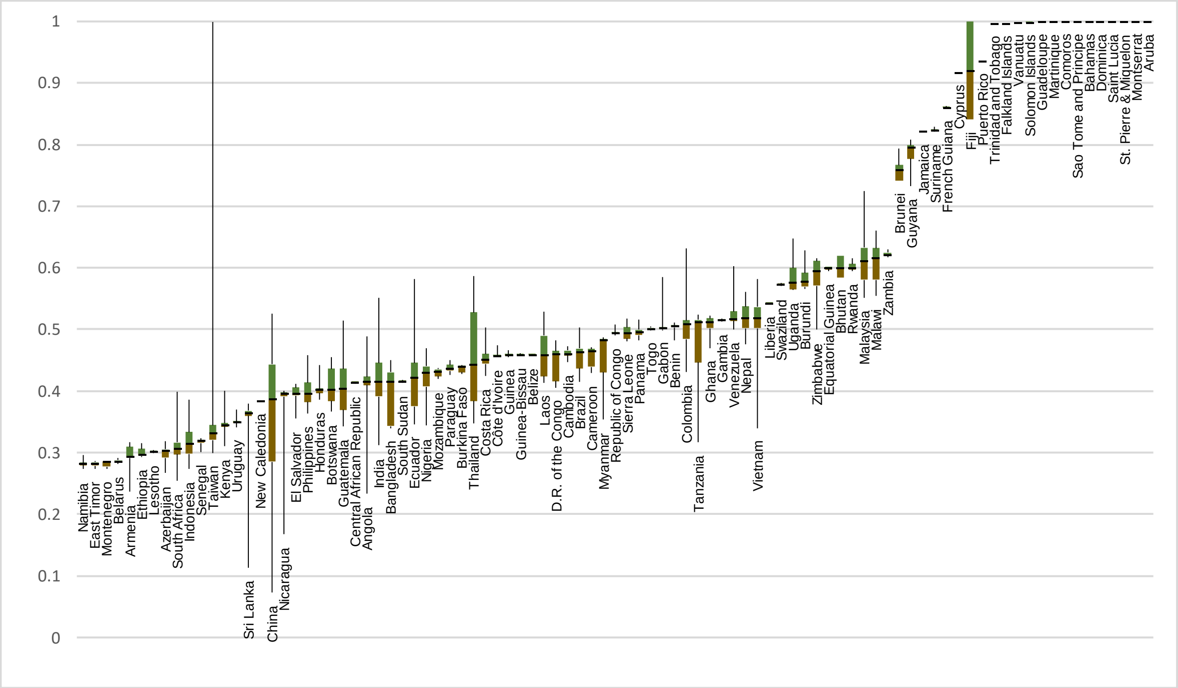


Figure 9. Boxplots for biodiversity value of lands in areas that fulfill each country's 30% transport energy demands by 2050, based on Scenario 1 (use of fresh, brackish and saltwater sources). Countries with median biodiversity values higher than the global median value (i.e., median biodiversity value ≥ 0.28) are included. Maximum and minimum values within countries are shown within the whiskers.

4. DISCUSSION

Current and future domestic transport energy demands can be partially fulfilled by microalgal biofuels, if reduction in their production costs allow their adoption (Slade and Bauen 2013, Zhu et al. 2017). However, their overall potential environmental impacts for satisfying domestic transport energy needs, including potential direct competition with food production and biodiversity, are largely unknown. Based on integer linear programming, we propose best areas for siting microalgal production farms for meeting a 30% domestic target for current and future transport energy production, aiming at reducing direct competition with agricultural lands and biodiversity. Furthermore, we identify countries where minimal overlap with high-value agricultural lands and biodiversity would occur while high lipid production levels are achieved, and explore potential conflicts with ecoregions of high ecological importance within these countries.

Our analyses show that direct competition among microalgal production, agricultural lands, and biodiversity, depend on the availability of areas with high potential microalgal biofuel productivities within countries, along with the availability of lands with low biodiversity and agricultural value in relation to each country's transport energy demands. Fulfilling 30% of current domestic transport energy demands would require 0.6% of global land area. However, microalgal production areas would be concentrated in countries with high energy consumption levels (i.e., 70% of microalgal production areas would occur within the USA, China, Russia, Germany, Canada, Japan, United Kingdom, India, Brazil, France, South Korea, Mexico, and Italy). Most of these countries do not offer large tracts of human-transformed dry lands for microalgal cultivation—which are less suitable for agricultural production (Alexandratos and Bruinsma 2012) and hold lower biodiversity values compared to more humid areas (Gaston 2000)—in relation to their high transport energy demands. This results in the global overlapping of microalgal production with areas of significant agricultural and biodiversity value (i.e., between 65% and 67% of microalgal production would overlap with mixed forests, grasslands, croplands, cropland/natural vegetation mosaics, and woody savannas). In contrast, previous analyses that do not consider national energy security targets show that best microalgal production areas globally would mostly overlap with barren and sparsely vegetation lands (i.e., dry areas) along coasts in North and East Africa, the Middle East, and western South America (Correa et al. 2019). Additionally, several of these countries are located within the temperate region (i.e., Russia, Germany, Canada, United Kingdom, France, South Korea, and Italy)—where biomass and lipid microalgal productivities are lower compared to tropical and subtropical regions as a result of fluctuating temperatures and solar irradiation (Moody et al. 2014, Venteris et al. 2014)—which would result in larger land footprints for fulfilling fixed domestic energy targets.

Microalgal biofuel production increases in low latitudes (Moody et al. 2014, Venteris et al. 2014). However, tropical and subtropical countries offer highly productive lands for future agricultural intensification and expansion (Alexandratos and Bruinsma 2012, Laurance 2015) and hold the highest biodiversity values globally (Dirzo and Raven 2003), which would increase the potential for conflicts among microalgal production, food production, and biodiversity in these areas (Correa et al. 2019). Countries located in low latitudes, and with available human-transformed dry areas (i.e., where agricultural and biodiversity value decrease) in relation to their domestic transport energy demands, would offer ideal conditions for fulfilling transport demands at lower direct competition with agriculture and biodiversity. In these set of countries—which mainly include emerging and developing economies within Africa, the Middle East, non-OECD Americas, and non-OECD Asia and Oceania—microalgal production would mostly overlap areas of lower agricultural and biodiversity values (i.e., between 90 and 92% of total microalgal production area would overlap with barren or sparsely vegetated lands and open shrublands, with median potential agricultural revenues of 75–108.5 USD ha^{-1}, a median number of 212–213 vertebrate species, and a median number of 3–4 threatened vertebrate species). Within these countries, less than 5% of each ecoregion of high ecological importance (Olson and Dinerstein 2002) would overlap microalgal production areas, mainly in arid and semiarid lands. However, even in these human-transformed dry areas, the minimization of environmental impacts driven by microalgal production, which include habitat loss for unique and threatened native species (Olson and Dinerstein 2002, Miles et al. 2006), should be considered.

The use of seawater could reduce competition with freshwater (Brauman et al. 2016), however, at higher competition with areas of higher agricultural value, with global median agricultural values increasing from 0.19 to 0.28 (i.e., from median potential agricultural revenues of 75 USD ha^{-1} to 108.5 USD ha^{-1}). Thus, future assessments on best areas for microalgal biofuels at national scales can consider trade-offs among freshwater consumption and agricultural value of lands, based on energy targets.

4.1 Future siting of microalgal production farms

Transport energy demands are expected to increase globally, leading to larger microalgal cultivation areas needed to fulfill each country's 30% domestic transport energy consumption (i.e., an increase in microalgal cultivation area between 56% and 58% compared to 2016 for Scenarios 1 and 2, respectively). Because the highest increases in microalgal production areas would occur in developing economies (i.e., mainly in India, Africa, non-OECD Asia and Oceania, non-OECD Americas, and the Middle East), potential conflicts with high-value agricultural lands and biodiverse areas would particularly intensify in tropical and subtropical regions (i.e., for Scenario 1, the overlapping among microalgal production areas with broadleaf forest, woody savannas, and savannas would increase by 148%, 104%, and 88%, respectively, and for Scenario 2, the overlapping with broadleaf forests would increase by 166%). Countries with available human-transformed dry lands in relation to their domestic transport energy demands in tropical and subtropical areas of the world, would offer low land footprints at the lowest competition with lands of high agricultural and biodiversity value (Figs. 6 and 8). As in 2016, these countries would be mainly located in Africa, the Middle East, non-OECD Americas, and non-OECD Asia and Oceania, mostly overlapping with barren or sparsely vegetated lands and open shrublands (i.e., ranging from 67% to 89% of total microalgal production area).

Overall, for both Scenarios 1 and 2, current and future scaling-up of microalgal biofuel production would lead to lower direct conflicts with food production and biodiversity (i.e., in relation to median values globally) within Australia, Chile, Djibouti, Egypt, Eritrea, Haiti, Iran, Iraq, Kuwait, Madagascar, Mauritania, Oman, Pakistan, Papua New Guinea, Qatar, Saudi Arabia, Somalia, Sudan, United Arab Emirates, and Yemen. However, some of these countries are constituted by islands (i.e., Haiti, Madagascar, and Papua New Guinea), where the extinction risk of native endemic species is highest compared to the mainland (Kier et al. 2009). Reducing targets in microalgal biofuel production would be an option for decreasing potential conflicts with local food production and endemic biodiversity in these island countries, particularly in Haiti, where a future 30% microalgal production target would require 1.2% of total land area.

While technological improvements (e.g., based on biorefinery systems and cultivation highly productive strains) (Chisti 2007, González-González et al. 2018) further reduce land footprints in countries with high energy demands, reducing targets in microalgal biofuel production (e.g., from 30% to 20% or 10%) can help to achieve substantial domestic transport energy demands at lower direct competition with food production and biodiversity. Furthermore, future assessments comparing microalgal biofuels with counterfactual biofuel production alternatives (e.g., maize, sugarcane, soybean, and oil palm), can guide the identification of biofuel alternatives that offer lowest potential competition with freshwater, food production and biodiversity for fulfilling increasing targets in transport energy demands (Correa et al. 2019). These analyses can consider microalgal biorefinery systems—in which food, animal feed, and biofuels can be produced (Uggetti et al. 2014, Vermuë et al. 2018)—that make use free CO_2 (i.e., from industries and anaerobic digesters) and nutrient sources (i.e., from wastewater), considering other measures of land value (e.g., ecosystem services, mining, and tourism).

5. CONCLUSIONS

Conflicts among microalgal biofuel production, high-value agricultural lands, and biodiverse areas, are expected to increase with higher domestic transport energy demands and lack of available human-transformed dry lands within countries. Countries with enough human-transformed dry lands in relation to their transport energy demands, are particularly promising for fulfilling larger domestic targets with microalgae at lower direct competition with food production and biodiversity. These conditions are met in a large set of developing economies in tropical and subtropical regions of the world, mainly located in Africa, the Middle East, non-OECD Americas, and non-OECD Asia and Oceania. Reducing targets in microalgal biofuel production would decrease potential conflicts with high-value agricultural lands and biodiversity in countries with high energy demands (e.g., in USA, China, Russia, Germany, Canada, Japan, United Kingdom, India, Brazil, France, South Korea, Mexico, and Italy), as well as in countries where future increases in transport energy demands are highest (e.g., developing economies within the tropics and subtropics), in tropical and subtropical countries without available human-transformed dry lands, and in island countries. In spite of the lower agricultural and biodiversity value of dry lands compared to more humid regions, and the smaller land footprint of microalgal production systems compared to food crops and second generation biofuels (Correa et al. 2017, Correa et al. 2019), the eventual expansion of microalgal production should consider the minimization of conflicts with the unique and important biodiversity of dry areas, particularly for threatened species. Further analyses based on free CO_2 (i.e., from industries anaerobic digesters) and nutrient sources (i.e., from wastewater), alternative land values (e.g., considering ecosystem services and several economic activities such as mining and tourism), and counterfactual biofuel production alternatives (e.g., food crops and second generation biofuels), can further refine the location of cost-effective areas for siting microalgal production farms at lowest environmental costs and at national scales.

ACKNOWLEDGEMENTS

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Chapter 3. Supplementary Information

1. Construction of layers for a global GIS model on microalgal profitability

A GIS-based multiple-criteria decision analysis (MCDA) was developed for constructing microalgal profitability layers (ranging from 0 to 1) for two cultivation scenarios: Scenario 1 (cultivation by using fresh/brackish/salt water sources) and Scenario 2 (cultivation by using seawater). Attributes that are essential for microalgal cultivation or that can maximize the profitability in microalgal biofuel production (i.e., water availability, lipid productivity, availability of flat lands, and proximity to main roads and railroads) (Chisti 2007, Schenk et al. 2008, Lundquist et al. 2010, Wigmosta et al. 2011, Slade and Bauen 2013, Venteris et al. 2014, Slegers et al. 2015) were considered for this analysis. In spite of reducing biofuel production costs, free CO_2 and nutrient sources (e.g., CO_2 from industries and anaerobic digesters, or nutrients from wastewater) were not included in the model, since they are inconsistently mapped globally and would limit the amount of land to reach fixed targets in domestic transport energy demands.

For constructing the final profitability layers, suitability layers representing each attribute (i.e., water availability, lipid productivity, availability of flat lands, and proximity to main roads and railroads) were overlaid in ArcGIS 10.5 based on the AND/OR Boolean operators. Without the use of weights, the AND Boolean operator retrieves the lowest value among pixels, while the OR Boolean operator retrieves the highest values among pixels. Fuzzy logic was applied for constructing each suitability layer, which based on the use of linear membership and sigmoid membership functions transforms input values into suitability values (i.e., ranging from 0 to 1) (Raines et al. 2010).

A linear function was defined as:

$$\mu(x) = 0 \; if \; x < min, \mu(x) = 1 \; if \; x > max$$

$$otherwise \; \mu(x) = \frac{(x - min)}{(max - min)}$$

Where x corresponds to each pixel value, max corresponds to the maximum value among pixels, and min corresponds to the minimum value among pixels.

A sigmoid function with large membership (i.e., larger input values result in higher suitability values) was defined as:

$$\mu(x) = \frac{1}{1 + \frac{x}{f_2}^{-f_1}}$$

A sigmoid function with small membership (i.e., smaller input values result in higher suitability values) was defined as:

$$\mu(x) = \frac{1}{1 + \frac{x}{f_2}^{f_1}}$$

Where f_1 is the spread of the function (defined as 5) and f_2 is the membership midpoint. The midpoints, which are assigned a membership value of 0.5, are shown in Table S1.

1.1 Microalgal profitability

Microalgal profitability resulted from overlaying water availability (i.e., fresh/brackish/salt water availability for Scenario 1, proximity to oceans for Scenario 2), along with lipid productivity, availability of flat lands, and proximity to transport networks, using the AND Boolean operator (Figs. S1 and S2). For Scenario 1, water availability (excluding oceans) after taking into account water depletion was overlaid with the aridity index—which corresponds to the ratio between mean annual precipitation and mean annual potential evapotranspiration (Trabucco and Zomer 2009)—and with the proximity to oceans, using the OR Boolean operator. Water availability excluding oceans was overlaid with water depletion driven by human activities (Brauman et al. 2016), using the AND Boolean operator. Water availability excluding oceans resulted from overlaying the proximity to rivers, proximity to irrigation dams, and proximity to fresh/brackish/salt groundwater sources, using the OR Boolean operator.

Considering restrictions in water use, a recharge/discharge membership midpoint of 1.8 km^3 year^{-1} was used for selecting suitable rivers, irrigation dams, and groundwater basins (Correa et al. 2019). For rivers, mean annual peak discharge was calculated. Thus, available water from rivers is expected to further decrease and limit microalgal cultivation.

The water depletion layer was obtained by rescaling the original water depletion percentages within watersheds obtained by Brauman et al. (2016) into suitability values ranging from 0 to 1 (Table S2). The proximity to rivers, irrigation dams, fresh/brackish/salt groundwater sources, oceans, and transport networks was based on the use of a cost layer (i.e., cost distance) based on slope, in which the slope was rescaled through a linear function into values ranging from 1 to 10.

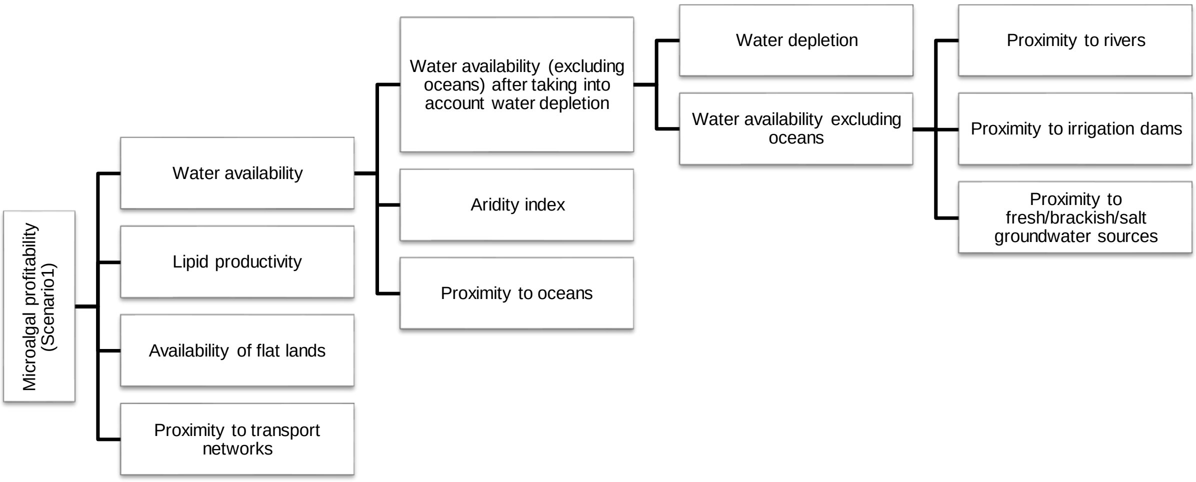

Figure S1. Overlaying of suitability layers for the development of a profitability model for siting microalgal farms for biodiesel production at a global scale. Scenario 1: Use of fresh, brackish or salt water.

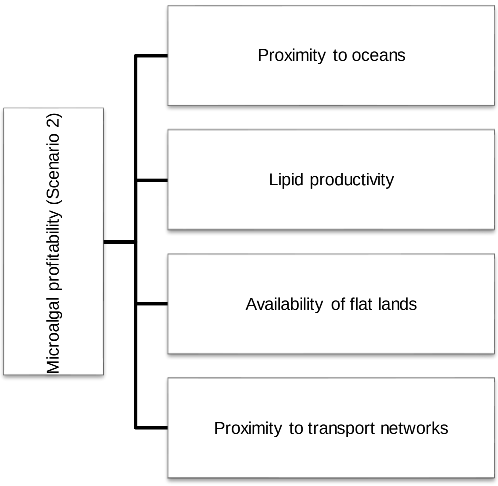

Figure S2. Overlaying of suitability layers for the development of a profitability model for siting microalgal farms for biodiesel production at a global scale. Scenario 2: Use of seawater.

1.2 Projection of rasters

Rasters were transformed into the Eckert-IV equal-area pseudocylindrical map projection. The potential annual gross economic rents from agricultural lands was resampled to a resolution of 5 × 5 km by using the Nearest Neighbor resampling method, while the number of vertebrate species, the number of threatened vertebrate species, and the number of species with small distribution ranges, were resampled to a resolution of 5 × 5 km based on the Bilinear Interpolation resampling method.

Table S1. Description of layers and membership functions used for the development of a profitability model for microalgal biofuel production and for the construction of layers on agricultural and biodiversity value. Sigmoid Large: larger entry values have higher suitability. Sigmoid Small: lower entry values have higher suitability. Not Applicable (NA).

Layers	Description	Original spatial resolution for rasters	Type of membership function	Membership midpoint	Source
Aridity index	Quantification of precipitation availability over atmospheric water demand. Aridity Index (AI) = MAP/MAE, where MAP = Mean Annual Precipitation and MAE = Mean Annual potential Evapotranspiration.	30 arcseconds	Sigmoid Large	1	Global aridity and PET database (Trabucco and Zomer 2009)
Proximity to rivers	Cost distance to permanent rivers with annual discharge ≥ 1.8 km^3 year$^{-1.}$ Based on annual peak discharge.	NA	Sigmoid Small	50 km	Layer based on HydroSHEDS (Lehner et al. 2008), Vmap0 for permanent streams http://gis-lab.info/qa/vmap0-eng.html and river bankfull width (Andreadis et al. 2013).
Proximity to irrigation dams	Cost distance to irrigation dams with annual recharge ≥ 1.8 km^3 year^{-1}	NA	Sigmoid Small	50 km	GRanDv1 database (Lehner et al. 2011)
Proximity to fresh/brackish/ salt groundwater sources	Cost distance to fresh/brackish/salt groundwater global aquifers with annual recharge ≥ 1.8 km^3 year^{-1}. Excludes areas with complex hydrogeological structures, and areas with local and shallow aquifers.	NA	Sigmoid Small	50 km	Groundwater Resources of the World 1: 25 000 000. (BGR & UNESCO 2008)
Water depletion	Water availability based on the fraction of renewable water consumptively used for human activities within a watershed.	NA	NA. See Table S2	NA	Layer based water depletion metric within watersheds (Brauman et al. 2016)
Proximity to oceans	Cost distance to oceans	NA	Sigmoid Small	50 km	Oceans v.3.00 http://www.naturalearthdata.com
Lipid productivity	Estimation of lipid productivity based on 4,388 lipid point estimates for the cultivation of *Nannochloropsis* sp. in photobioreactors (Moody et al. 2014), using as predictors mean annual radiation and the residuals of mean annual temperature explained by radiation. Future mean annual temperature (by 2050) was obtained based on an ensemble model for the Representative Concentration Pathway (RCP) 8.5 (i.e., high emissions scenario), by averaging mean annual temperatures among the following General Circulation Models (GCMs): BCC-CSM1-1, CCSM4, GISS-E2-R, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM-CHEM, MRI-CGCM3, and NorESM1-M (Hijmans et al. 2005).	5 × 5 km	Linear	NA	Layer based on lipid productivity estimates (Moody et al. 2014), and WorldClim v.1.4 and v2 (Hijmans et al. 2005).
Availability of flat lands	Terrain slope	30 arcseconds	Sigmoid Small	5°	Layer derived from GTOPO30 DEM https://lta.cr.usgs.gov/GTOPO30
Proximity to transport networks	Cost distance to roads and railroads	NA	Sigmoid Small	50 km	Roads and railroads v. 3.0.0 http://www.naturalearthdata.com
Agricultural value	Potential annual gross economic rents from agricultural lands	300 arcseconds	Linear	NA	Potential annual gross economic rents from agricultural lands (Naidoo and Iwamura 2007)
Number of vertebrate species	Number of vertebrate species (considering amphibians, birds, and mammals) based on IUCN species distribution maps, Bird Life International, and Nature Serve	10 × 10 km	Linear	NA	Biodiversity maps (Jenkins et al. 2013)
Number of threatened vertebrate species	Number of threatened vertebrate species (considering amphibians, birds, and mammals) based on IUCN distribution maps, Bird Life International, and Nature Serve	10 × 10 km	Linear	NA	Biodiversity maps (Jenkins et al. 2013)
Number of vertebrate species with small distribution ranges	Number of vertebrate species with small distribution ranges (considering amphibians, birds, and mammals) based on IUCN distribution maps, Bird Life International, and Nature Serve	10 × 10 km	Linear	NA	Biodiversity maps (Jenkins et al. 2013)
Presence of islands	Islands	NA	Sigmoid Small	15,000 km^2	Layer based on GADM database http://gadm.org/

Presence of areas with low human pressures	Measure of human pressures (no pressure, low pressure, moderate pressure, high pressure, very high pressure) based on the presence of built environments, croplands, pastures, human population density, night-time lights, railways, roads, and navigable waterways.	1 × 1 km	Sigmoid Small	4	Human footprint (Venter et al. 2016)
Presence of mangroves	Percentage of mangroves covering each pixel (i.e., 25 km^2)	NA	Linear	NA	Global distribution of mangroves (Giri et al. 2011)

1.3 Future aridity index and lipid productivity

For each Representative Concentration Pathway (RCP) (i.e., 2.6, 4.6, 6.0, and 8.5) we constructed an ensemble model by averaging mean monthly temperatures, minimum monthly temperatures, maximum monthly temperatures, and mean annual precipitation values among the following General Circulation Models (GCMs): BCC-CSM1-1, CCSM4, GISS-E2-R, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM-CHEM, MRI-CGCM3, and NorESM1-M (Hijmans et al. 2005). The RCP 8.5, which corresponds to a high emissions scenario (Riahi et al. 2011), was used to find potential microalgal production areas with high profitabilities and low direct competition with food production and biodiversity by 2050. A difference in radiative forcing of around 2 W m^{-2} (i.e., equivalent to about 1° C in global mean surface air temperature) is predicted between the low emissions RCP 2.5 and the high emissions RCP 8.5 by 2050 (van Vuuren et al. 2011, Pachauri et al. 2014). This change did not substantially alter best areas for growing microalgae globally.

The aridity index was calculated by dividing the mean annual precipitation by the mean annual potential evapotranspiration (Trabucco and Zomer 2009). The mean daily potential evapotranspiration was calculated based on the Hargreaves model (Hargreaves and Samani 1985, Hargreaves and Allen 2003), which has been considered suitable for predicting potential evapotranspiration globally (Trabucco and Zomer 2009).

$$PET = 0.0023 * RA * (T + 17.8) * TR^{0.5}$$

Where PET (mm day^{-1}) is daily potential evapotranspiration, RA is the extra-terrestrial radiation (expressed in mm day^{-1}), T is the mean daily temperature (°C), and TR is the mean daily temperature range as a proxy to describe the effect of cloud cover on the quantity of extra-terrestrial radiation that reaches the land surface (Trabucco and Zomer 2009). Because daily means for the several variables are not available, monthly means are used. The summation of the daily PET along the year resulted in the annual potential evapotranspiration.

A multiple linear regression model was developed to predict lipid productivity globally by using 4,388 lipid point productivity estimates for the cultivation of *Nannochloropsis* sp. in photobioreactors (Moody et al. 2014). We used the package “raster” (Hijmans et al. 2017) and the software R 3.4.2, using as predictors the mean annual radiation and the residuals of mean annual temperature explained by radiation (Hijmans et al. 2005, Fick and Hijmans 2017), allowing the estimation of lipid productivities in areas with lower density in point estimates (e.g., mountains) (Correa et al. 2019). The future mean annual temperature was obtained based on the RCP 8.5 ensemble model.

1.4 Agricultural and biodiversity value

The agricultural value (i.e., the potential annual gross economic rents from agricultural lands) was rescaled using a linear function with a maximum value of 800 USD ha^{-1}, which corresponds to highly profitable lands (Naidoo and Iwamura 2007). Biodiversity value resulted from overlaying the number of vertebrate species, the number of threatened vertebrate species, and the number of vertebrate species with small distribution ranges (i.e., considering amphibians, birds, and mammals) (Jenkins et al. 2013), along with the presence of islands (which compared to the mainland harbor more endemic species and populations) (Kier et al. 2009, Tershy et al. 2015, McCreless et al. 2016), the presence of areas with low human pressures (i.e., based on the Global Human Footprint) (Venter et al. 2016), and the presence of mangroves (Giri et al. 2011), using the OR Boolean operator.

Table S2. Reclassification of original values for water depletion categories (Brauman et al. 2016) into suitability values ranging from 0 to 1.

Water depletion categories	Suitability values
<5% depleted	0.95
5–25% depleted	0.75
25–50% depleted	0.5
50–75% depleted	0.25
Dry-year depleted	0.25
Seasonally depleted	0.25
75–100% depleted	0
100% depleted	0

2. Countries included in the analyses

Table S3 shows the different countries included in the analyses. Here, countries are defined as sovereign states or administrative units with an associated ISO based on the GADM database v.2. The following countries—which excluding the Antartica and Greenland represent 0.25% of global land area—were not considered: Åland, American Samoa, Andorra, Antarctica, Bouvet Island, British Indian Ocean Territory, Christmas Island, Cocos Islands, Faroe Islands, French Southern Territories, Greenland, Guam, Guernsey, Heard Island and McDonald Islands, Isle of Man, Jersey, Liechtenstein, Marshall Islands, Mayotte, Micronesia, Monaco, Nauru, Niue, Norfolk Island, Northern Mariana Islands, Palau, Palestina, Pitcairn Islands, Saint Helena, Saint-Barthélemy, Saint-Martin, San Marino, South Georgia and the South Sandwich Islands, Spratly islands, Svalbard and Jan Mayen, Tokelau, Tuvalu, United States Minor Outlying Islands, Vatican City, Virgin Islands U.S., Wallis and Futuna, and Western Sahara.

Table S3. Current and future transport energy demands for the different countries included in the analyses. The annual growth on transport energy consumption is shown per economic region (EIA 2016). Following EIA (2016), Turkey and Israel are considered part of OECD Europe. Million tonnes of oil equivalent (MTOE).

ISO	Country	Region	Landlocked	Annual increase in transport demands (%)	Transport demands 2016 (MTOE)	Transport demands 2050 (MTOE)
DZA	Algeria	Africa	No	3.1	15.13	42.72
AGO	Angola	Africa	No	3.1	2.75	7.77
BEN	Benin	Africa	No	3.1	1.59	4.49
BWA	Botswana	Africa	Yes	3.1	0.83	2.34
BFA	Burkina Faso	Africa	Yes	3.1	0.43	1.21
BDI	Burundi	Africa	Yes	3.1	0.24	0.68
CMR	Cameroon	Africa	No	3.1	1.08	3.05
CPV	Cape Verde	Africa	No	3.1	0.01	0.03
CAF	Central African Republic	Africa	Yes	3.1	0.10	0.29
TCD	Chad	Africa	Yes	3.1	0.33	0.94
COM	Comoros	Africa	No	3.1	0.02	0.05
CIV	Côte d'Ivoire	Africa	No	3.1	1.20	3.39
COD	Democratic Republic of the	Africa	No	3.1	0.63	1.78
DJI	Djibouti	Africa	No	3.1	0.02	0.06
EGY	Egypt	Africa	No	3.1	18.69	52.77
GNQ	Equatorial Guinea	Africa	No	3.1	0.03	0.08
ERI	Eritrea	Africa	No	3.1	0.06	0.17
ETH	Ethiopia	Africa	Yes	3.1	1.74	4.91
GAB	Gabon	Africa	No	3.1	0.27	0.76
GMB	Gambia	Africa	No	3.1	0.05	0.13
GHA	Ghana	Africa	No	3.1	2.42	6.83
GIN	Guinea	Africa	No	3.1	0.28	0.80
GNB	Guinea-Bissau	Africa	No	3.1	0.04	0.12
KEN	Kenya	Africa	No	3.1	2.94	8.30
LSO	Lesotho	Africa	Yes	3.1	0.05	0.14
LBR	Liberia	Africa	No	3.1	0.11	0.30
LBY	Libya	Africa	No	3.1	7.09	20.02
MDG	Madagascar	Africa	No	3.1	0.57	1.61
MWI	Malawi	Africa	Yes	3.1	0.42	1.17
MLI	Mali	Africa	Yes	3.1	0.41	1.17
MRT	Mauritania	Africa	No	3.1	0.10	0.28
MUS	Mauritius	Africa	No	3.1	0.38	1.07
MAR	Morocco	Africa	No	3.1	5.58	15.76
MOZ	Mozambique	Africa	No	3.1	1.28	3.61
NAM	Namibia	Africa	No	3.1	0.75	2.12
NER	Niger	Africa	Yes	3.1	0.39	1.10
NGA	Nigeria	Africa	No	3.1	17.25	48.71
COG	Republic of Congo	Africa	No	3.1	0.67	1.89
REU	Reunion	Africa	No	3.1	0.02	0.05
RWA	Rwanda	Africa	Yes	3.1	0.27	0.77
STP	Sao Tome and Principe	Africa	No	3.1	0.01	0.01
SEN	Senegal	Africa	No	3.1	0.97	2.74
SYC	Seychelles	Africa	No	3.1	0.00	0.01
SLE	Sierra Leone	Africa	No	3.1	0.17	0.48
SOM	Somalia	Africa	No	3.1	0.33	0.93
ZAF	South Africa	Africa	No	3.1	18.80	53.08
SSD	South Sudan	Africa	Yes	3.1	0.32	0.90
SDN	Sudan	Africa	No	3.1	3.14	8.87

SWZ	Swaziland	Africa	No	3.1	0.03	0.09
TZA	Tanzania	Africa	No	3.1	2.30	6.49
TGO	Togo	Africa	No	3.1	0.51	1.44
TUN	Tunisia	Africa	No	3.1	2.45	6.92
UGA	Uganda	Africa	Yes	3.1	0.96	2.70
ZMB	Zambia	Africa	Yes	3.1	0.40	1.13
ZWE	Zimbabwe	Africa	Yes	3.1	0.64	1.81
BHR	Bahrain	Middle East	No	1.9	1.22	2.31
IRN	Iran	Middle East	No	1.9	44.84	85.03
IRQ	Iraq	Middle East	No	1.9	8.49	16.10
JOR	Jordan	Middle East	No	1.9	2.77	5.25
KWT	Kuwait	Middle East	No	1.9	4.79	9.08
LBN	Lebanon	Middle East	No	1.9	1.95	3.70
OMN	Oman	Middle East	No	1.9	4.17	7.91
QAT	Qatar	Middle East	No	1.9	4.37	8.29
SAU	Saudi Arabia	Middle East	No	1.9	45.80	86.85
SYR	Syria	Middle East	No	1.9	2.15	4.08
ARE	United Arab Emirates	Middle East	No	1.9	11.69	22.17
YEM	Yemen	Middle East	No	1.9	0.94	1.78
AIA	Anguilla	non-OECD Americas	No	2.5	0.00	0.01
ATG	Antigua and Barbuda	non-OECD Americas	No	2.5	0.03	0.07
ARG	Argentina	non-OECD Americas	No	2.5	17.51	40.54
ABW	Aruba	non-OECD Americas	No	2.5	0.03	0.07
BHS	Bahamas	non-OECD Americas	No	2.5	0.11	0.25
BRB	Barbados	non-OECD Americas	No	2.5	0.08	0.18
BLZ	Belize	non-OECD Americas	No	2.5	0.10	0.24
BMU	Bermuda	non-OECD Americas	No	2.5	0.02	0.04
BOL	Bolivia	non-OECD Americas	Yes	2.5	2.86	6.62
BES	Bonaire, Saint Eustatius and Saba	non-OECD Americas	No	2.5	0.01	0.02
BRA	Brazil	non-OECD Americas	No	1.7	82.96	147.16
VGB	British Virgin Islands	non-OECD Americas	No	2.5	0.01	0.02
CYM	Cayman Islands	non-OECD Americas	No	2.5	0.02	0.04
COL	Colombia	non-OECD Americas	No	2.5	10.65	24.66
CRI	Costa Rica	non-OECD Americas	No	2.5	1.89	4.38
CUB	Cuba	non-OECD Americas	No	2.5	0.55	1.27
CUW	Curaçao	non-OECD Americas	No	2.5	0.36	0.83
DMA	Dominica	non-OECD Americas	No	2.5	0.02	0.05
DOM	Dominican Republic	non-OECD Americas	No	2.5	2.04	4.72
ECU	Ecuador	non-OECD Americas	No	2.5	5.58	12.92
SLV	El Salvador	non-OECD Americas	No	2.5	1.17	2.71
FLK	Falkland Islands	non-OECD Americas	No	2.5	0.00	0.00
GUF	French Guiana	non-OECD Americas	No	2.5	0.07	0.17
GRD	Grenada	non-OECD Americas	No	2.5	0.03	0.07
GLP	Guadeloupe	non-OECD Americas	No	2.5	0.13	0.29
GTM	Guatemala	non-OECD Americas	No	2.5	2.69	6.23
GUY	Guyana	non-OECD Americas	No	2.5	0.22	0.50
HTI	Haiti	non-OECD Americas	No	2.5	0.47	1.09
HND	Honduras	non-OECD Americas	No	2.5	1.36	3.15
JAM	Jamaica	non-OECD Americas	No	2.5	0.64	1.48
MTQ	Martinique	non-OECD Americas	No	2.5	0.11	0.25
MSR	Montserrat	non-OECD Americas	No	2.5	0.00	0.00
NIC	Nicaragua	non-OECD Americas	No	2.5	0.78	1.81
PAN	Panama	non-OECD Americas	No	2.5	1.56	3.61
PRY	Paraguay	non-OECD Americas	Yes	2.5	2.13	4.93
PER	Peru	non-OECD Americas	No	2.5	7.87	18.22
PRI	Puerto Rico	non-OECD Americas	No	2.5	0.92	2.14
KNA	Saint Kitts and Nevis	non-OECD Americas	No	2.5	0.02	0.04
LCA	Saint Lucia	non-OECD Americas	No	2.5	0.05	0.12
SPM	Saint Pierre and Miquelon	non-OECD Americas	No	2.5	0.00	0.00
VCT	Saint Vincent and the Grenadines	non-OECD Americas	No	2.5	0.03	0.07
SMX	Sint Maarten	non-OECD Americas	No	2.5	0.01	0.03
SUR	Suriname	non-OECD Americas	No	2.5	0.20	0.46
TTO	Trinidad and Tobago	non-OECD Americas	No	2.5	1.24	2.87

TCA	Turks and Caicos Islands	non-OECD Americas	No	2.5	0.01	0.02
URY	Uruguay	non-OECD Americas	No	2.5	1.28	2.96
VEN	Venezuela	non-OECD Americas	No	2.5	13.62	31.54
AFG	Afghanistan	non-OECD Asia and Oceania	Yes	2.9	2.73	7.20
BGD	Bangladesh	non-OECD Asia and Oceania	No	2.9	3.45	9.12
BTN	Bhutan	non-OECD Asia and Oceania	Yes	2.9	0.06	0.16
BRN	Brunei	non-OECD Asia and Oceania	No	2.9	0.45	1.19
KHM	Cambodia	non-OECD Asia and Oceania	No	2.9	1.68	4.44
CHN	China	non-OECD Asia and Oceania	No	2.7	298.19	737.71
COK	Cook Islands	non-OECD Asia and Oceania	No	2.9	0.00	0.00
TLS	East Timor	non-OECD Asia and Oceania	No	2.9	0.10	0.26
FJI	Fiji	non-OECD Asia and Oceania	No	2.9	0.07	0.18
PYF	French Polynesia	non-OECD Asia and Oceania	No	2.9	0.02	0.06
HKG	Hong Kong	non-OECD Asia and Oceania	No	2.9	2.58	6.82
IND	India	non-OECD Asia and Oceania	No	4.4	89.95	388.88
IDN	Indonesia	non-OECD Asia and Oceania	No	2.9	47.25	124.89
KIR	Kiribati	non-OECD Asia and Oceania	No	2.9	0.01	0.02
LAO	Laos	non-OECD Asia and Oceania	Yes	2.9	0.53	1.39
MAC	Macao	non-OECD Asia and Oceania	No	2.9	0.05	0.13
MYS	Malaysia	non-OECD Asia and Oceania	No	2.9	21.58	57.04
MDV	Maldives	non-OECD Asia and Oceania	No	2.9	0.03	0.09
MNG	Mongolia	non-OECD Asia and Oceania	Yes	2.9	0.58	1.53
MM	Myanmar	non-OECD Asia and Oceania	No	2.9	1.71	4.52
NPL	Nepal	non-OECD Asia and Oceania	Yes	2.9	1.28	3.38
NCL	New Caledonia	non-OECD Asia and Oceania	No	2.9	0.02	0.06
PRK	North Korea	non-OECD Asia and Oceania	No	2.9	0.48	1.27
PAK	Pakistan	non-OECD Asia and Oceania	No	2.9	15.66	41.39
PNG	Papua New Guinea	non-OECD Asia and Oceania	No	2.9	0.63	1.67
PHL	Philippines	non-OECD Asia and Oceania	No	2.9	11.46	30.29
WSM	Samoa	non-OECD Asia and Oceania	No	2.9	0.02	0.04
SGP	Singapore	non-OECD Asia and Oceania	No	2.9	2.37	6.26
SLB	Solomon Islands	non-OECD Asia and Oceania	No	2.9	0.05	0.12
LKA	Sri Lanka	non-OECD Asia and Oceania	No	2.9	3.10	8.19
TWN	Taiwan	non-OECD Asia and Oceania	No	2.9	12.83	33.91
THA	Thailand	non-OECD Asia and Oceania	No	2.9	25.20	66.61
TON	Tonga	non-OECD Asia and Oceania	No	2.9	0.01	0.02
VUT	Vanuatu	non-OECD Asia and Oceania	No	2.9	0.02	0.06
VNM	Vietnam	non-OECD Asia and Oceania	No	2.9	12.28	32.46
ALB	Albania	non-OECD Europe and Eurasia	No	1	0.83	1.16
ARM	Armenia	non-OECD Europe and Eurasia	Yes	1	0.62	0.87
AZE	Azerbaijan	non-OECD Europe and Eurasia	Yes	1	2.27	3.18
BLR	Belarus	non-OECD Europe and Eurasia	Yes	1	3.79	5.32
BIH	Bosnia and Herzegovina	non-OECD Europe and Eurasia	No	1	1.19	1.67
BGR	Bulgaria	non-OECD Europe and Eurasia	No	1	3.29	4.61
HRV	Croatia	non-OECD Europe and Eurasia	No	1	2.05	2.88
CYP	Cyprus	non-OECD Europe and Eurasia	No	1	0.65	0.91
GEO	Georgia	non-OECD Europe and Eurasia	No	1	1.46	2.05
GIB	Gibraltar	non-OECD Europe and Eurasia	No	1	0.15	0.21
KAZ	Kazakhstan	non-OECD Europe and Eurasia	Yes	1	5.47	7.67
KO-	Kosovo	non-OECD Europe and Eurasia	Yes	1	0.39	0.55
KGZ	Kyrgyzstan	non-OECD Europe and Eurasia	Yes	1	1.14	1.60
LTU	Lithuania	non-OECD Europe and Eurasia	No	1	1.87	2.62
MKD	Macedonia	non-OECD Europe and Eurasia	Yes	1	0.68	0.95
MLT	Malta	non-OECD Europe and Eurasia	No	1	0.20	0.28
MDA	Moldova	non-OECD Europe and Eurasia	Yes	1	0.69	0.97
MNE	Montenegro	non-OECD Europe and Eurasia	No	1	0.22	0.31
ROU	Romania	non-OECD Europe and Eurasia	No	1	5.82	8.16
RUS	Russia	non-OECD Europe and Eurasia	No	1	94.29	132.25
SRB	Serbia	non-OECD Europe and Eurasia	Yes	1	2.03	2.85
TJK	Tajikistan	non-OECD Europe and Eurasia	Yes	1	0.43	0.60
TKM	Turkmenistan	non-OECD Europe and Eurasia	Yes	1	4.33	6.07
UKR	Ukraine	non-OECD Europe and Eurasia	No	1	9.18	12.88
UZB	Uzbekistan	non-OECD Europe and Eurasia	Yes	1	2.24	3.14

CAN	Canada	OECD Americas	No	0.1	61.13	63.24
CHL	Chile	OECD Americas	No	1.2	8.84	13.26
MEX	Mexico	OECD Americas	No	1.2	52.94	79.42
USA	United States	OECD Americas	No	0.1	626.10	647.74
AUS	Australia	OECD Asia and Oceania	No	1	32.92	46.17
JPN	Japan	OECD Asia and Oceania	No	-0.7	72.41	57.03
NZL	New Zealand	OECD Asia and Oceania	No	1	4.89	6.86
KOR	South Korea	OECD Asia and Oceania	No	0.8	35.42	46.44
AUT	Austria	OECD Europe	Yes	0.2	8.58	9.18
BEL	Belgium	OECD Europe	No	0.2	9.09	9.73
CZE	Czech Republic	OECD Europe	Yes	0.2	6.53	6.99
DNK	Denmark	OECD Europe	No	0.2	4.19	4.49
EST	Estonia	OECD Europe	No	0.2	0.79	0.85
FIN	Finland	OECD Europe	No	0.2	4.31	4.61
FRA	France	OECD Europe	No	0.2	44.06	47.16
DEU	Germany	OECD Europe	No	0.2	57.17	61.19
GRC	Greece	OECD Europe	No	0.2	5.92	6.34
HUN	Hungary	OECD Europe	Yes	0.2	4.37	4.68
ISL	Iceland	OECD Europe	No	0.2	0.33	0.35
IRL	Ireland	OECD Europe	No	0.2	4.05	4.34
ISR	Israel	OECD Europe	No	0.2	5.87	6.28
ITA	Italy	OECD Europe	No	0.2	36.13	38.67
LVA	Latvia	OECD Europe	No	0.2	1.07	1.15
LUX	Luxembourg	OECD Europe	Yes	0.2	1.93	2.07
NLD	Netherlands	OECD Europe	No	0.2	10.47	11.21
NOR	Norway	OECD Europe	No	0.2	4.81	5.15
POL	Poland	OECD Europe	No	0.2	18.67	19.98
PRT	Portugal	OECD Europe	No	0.2	5.61	6.00
SVK	Slovakia	OECD Europe	Yes	0.2	2.45	2.62
SVN	Slovenia	OECD Europe	No	0.2	1.88	2.01
ESP	Spain	OECD Europe	No	0.2	30.83	33.00
SWE	Sweden	OECD Europe	No	0.2	8.22	8.80
CHE	Switzerland	OECD Europe	Yes	0.2	5.72	6.12
TUR	Turkey	OECD Europe	No	0.2	26.69	28.57
GBR	United Kingdom	OECD Europe	No	0.2	41.09	43.98

3. Countries with high productivities and lower direct competition with high-value agricultural lands and biodiversity

Best countries for siting microalgal biofuel production farms (i.e., high potential lipid productivities) at the lowest direct competition with high-value agricultural and biodiverse lands are shown for Scenario 1 (Tables S4, S5) and Scenario 2 (Tables S6, S7).

Table S4. Countries that offer higher potential lipid productivities (i.e., median values higher than 20.3 m^3 ha^{-1} $year^{-1}$) with lower direct competition with agricultural lands (i.e., median agricultural values lower than 0.19) in 2016 for Scenario 1 (i.e., use of fresh/brackish and salt water for microalgal cultivation).

Region	Country	Median lipid productivity (m^3 ha^{-1} $year^{-1}$)	Median agricultural value
Africa	Chad	24.0	0.00
Africa	Egypt	23.3	0.00
Africa	Namibia	21.8	0.00
Africa	Algeria	20.4	0.00
Africa	Sudan	23.7	0.00
Africa	Eritrea	24.0	0.00
Africa	Somalia	24.5	0.00

Africa	South Africa	21.5	0.00
Africa	Djibouti	24.2	0.00
Africa	Mauritania	23.9	0.00
Africa	Mali	24.1	0.01
Africa	Niger	23.4	0.01
Africa	Kenya	22.8	0.01
Africa	Botswana	22.1	0.02
Africa	Togo	22.1	0.06
Africa	Senegal	23.9	0.09
Africa	Ethiopia	23.3	0.09
Africa	Madagascar	22.7	0.10
Africa	Guinea	22.5	0.17
Middle East	United Arab Emirates	23.7	0.00
Middle East	Oman	23.3	0.00
Middle East	Yemen	24.0	0.00
Middle East	Iran	22.1	0.00
Middle East	Saudi Arabia	22.9	0.00
Middle East	Iraq	21.1	0.00
Middle East	Qatar	21.7	0.00
Middle East	Bahrain	21.6	0.00
Middle East	Kuwait	21.5	0.03
non-OECD Americas	Venezuela	22.1	0.03
non-OECD Americas	Haiti	21.1	0.10
non-OECD Asia and Oceania	Pakistan	21.8	0.00
non-OECD Asia and Oceania	Vanuatu	21.0	0.10
non-OECD Asia and Oceania	Solomon Islands	21.5	0.10
non-OECD Asia and Oceania	Papua New Guinea	21.7	0.16
OECD Americas	Chile	20.5	0.00
OECD Asia and Oceania	Australia	24.1	0.01

Table S5. Countries that offer higher potential lipid productivities (i.e., median values higher than 20.3 m^3 ha^{-1} year^{-1}) with lower direct competition with biodiverse lands (i.e., median biodiversity values lower than 0.28) in 2016 for Scenario 1 (i.e., use of fresh/brackish and salt water for microalgal cultivation).

Region	**Country**	**Median lipid productivity (m^3 ha^{-1} year^{-1})**	**Median biodiversity value**
Africa	Mauritania	23.9	0.09
Africa	Sudan	23.7	0.11
Africa	Egypt	23.3	0.12
Africa	Algeria	20.4	0.12
Africa	Somalia	24.5	0.14
Africa	Madagascar	22.7	0.16
Africa	Chad	24.0	0.17
Africa	Niger	23.4	0.22
Africa	Mali	24.1	0.25
Africa	Namibia	21.8	0.27
Africa	Djibouti	24.2	0.27
Africa	Eritrea	24.0	0.28
Middle East	Iraq	21.1	0.06
Middle East	Bahrain	21.6	0.06
Middle East	Yemen	24.0	0.10
Middle East	Qatar	21.7	0.11
Middle East	Saudi Arabia	22.9	0.12
Middle East	Kuwait	21.5	0.12
Middle East	United Arab Emirates	23.7	0.13
Middle East	Oman	23.3	0.15
Middle East	Iran	22.1	0.17
non-OECD Americas	Dominican Republic	21.0	0.20
non-OECD Americas	Haiti	21.1	0.22
non-OECD Americas	Cuba	22.1	0.26

non-OECD Asia and Oceania	Pakistan	21.8	0.17
non-OECD Asia and Oceania	Papua New Guinea	21.7	0.24
OECD Americas	Chile	20.5	0.08
OECD Asia and Oceania	Australia	24.1	0.23

Table S6. Countries that offer higher potential lipid productivities (i.e., median values higher than 20.2 m^3 ha^{-1} $year^{-1}$) with lower direct competition with agricultural lands (i.e., median agricultural values lower than 0.28) in 2016 for Scenario 2 (i.e., use of seawater for microalgal cultivation).

Region	Country	Median lipid productivity (m^3 ha^{-1} $year^{-1}$)	Median agricultural value
Africa	Egypt	22.3	0.00
Africa	Sudan	22.4	0.00
Africa	Eritrea	24.0	0.00
Africa	Somalia	24.5	0.00
Africa	Djibouti	24.2	0.00
Africa	Mauritania	22.6	0.00
Africa	Senegal	22.4	0.08
Africa	Madagascar	22.0	0.17
Africa	Gambia	22.5	0.19
Middle East	United Arab Emirates	23.7	0.00
Middle East	Oman	23.3	0.00
Middle East	Yemen	24.0	0.00
Middle East	Iran	22.2	0.00
Middle East	Saudi Arabia	22.9	0.00
Middle East	Qatar	21.7	0.00
Middle East	Bahrain	21.6	0.00
Middle East	Iraq	21.1	0.02
Middle East	Kuwait	21.5	0.03
non-OECD Americas	Venezuela	22.1	0.03
non-OECD Americas	Haiti	21.1	0.10
non-OECD Americas	Jamaica	22.2	0.27
non-OECD Asia and Oceania	Pakistan	21.8	0.00
non-OECD Asia and Oceania	Vanuatu	21.0	0.10
non-OECD Asia and Oceania	Solomon Islands	21.5	0.10
non-OECD Asia and Oceania	Papua New Guinea	21.7	0.16
non-OECD Asia and Oceania	Cambodia	20.8	0.24
OECD Americas	Chile	20.5	0.00
OECD Americas	Mexico	20.2	0.02
OECD Asia and Oceania	Australia	24.0	0.01

Table S7. Countries that offer higher potential lipid productivities (i.e., median values higher than 20.2 m^3 ha^{-1} $year^{-1}$) with lower direct competition with biodiverse lands (i.e., median biodiversity values lower than 0.28) in 2016 for Scenario 2 (i.e., use of seawater for microalgal cultivation).

Region	Country	Median lipid productivity (m^3 ha^{-1} $year^{-1}$)	Median biodiversity value
Africa	Egypt	22.3	0.12
Africa	Somalia	24.5	0.14
Africa	Sudan	22.4	0.15
Africa	Mauritania	22.6	0.16
Africa	Madagascar	22.0	0.18
Africa	Djibouti	24.2	0.27
Africa	Eritrea	24.0	0.28
Middle East	Bahrain	21.6	0.06
Middle East	Yemen	24.0	0.10
Middle East	Qatar	21.7	0.11
Middle East	Saudi Arabia	22.9	0.12
Middle East	Kuwait	21.5	0.12
Middle East	United Arab Emirates	23.7	0.13

Middle East	Oman	23.3	0.15
Middle East	Iran	22.2	0.17
Middle East	Iraq	21.1	0.19
non-OECD Americas	Dominican Republic	21.0	0.20
non-OECD Americas	Haiti	21.1	0.22
non-OECD Americas	Cuba	22.1	0.26
non-OECD Asia and Oceania	Pakistan	21.8	0.17
non-OECD Asia and Oceania	Papua New Guinea	21.7	0.24
non-OECD Asia and Oceania	East Timor	22.5	0.28
OECD Americas	Chile	20.5	0.08
OECD Americas	Mexico	20.2	0.24
OECD Asia and Oceania	Australia	24.0	0.23

Table S8 shows the overlapping among microalgal cultivation areas and ecoregions of high ecological priority (Olson and Dinerstein 2002) for Scenarios 1 and 2.

Table S8. Microalgal production areas that fulfill each country's 30% transport energy demands in 2016 and 2050 and overlap priority ecoregions for global conservation (i.e., Global 200 ecoregions) (Olson and Dinerstein 2002). Countries where higher microalgal productivities (HP) can be achieved at lower competition with agriculture (LA) and biodiversity (LB) are considered for Scenarios 1 (i.e., use of fresh, brackish and salt water) and 2 (i.e., use of seawater). Median microalgal lipid productivity > 20.3, 20.2, 20.1, and 19.9 m^3 ha^{-1} $year^{-1}$ for Scenario 1 in 2016, Scenario 2 in 2016, Scenario 1 in 2050, and Scenario 2 in 2050, respectively. Median agricultural values < 0.19, 0.28, 0.22, and 0.28 for Scenario 1 in 2016, Scenario 2 in 2016, Scenario 1 in 2050, and Scenario 2 in 2050, respectively. Median biodiversity values < 0.28, 0.28, 0.28, and 0.31 for Scenario 1 in 2016, Scenario 2 in 2016, Scenario 1 in 2050, and Scenario 2 in 2050, respectively. Microalgal production areas (km^2) and their percentages in relation to total microalgal production areas are included.

Ecoregions		**2016**								**2050**							
		Scen. 1 HP-LA		**Scen. 1 HP-LB**		**Scen. 2 HP-LA**		**Scen. 2 HP-LB**		**Scen. 1 HP-LA**		**Scen. 1 HP-LB**		**Scen. 2 HP-LA**		**Scen. 2 HP-LB**	
	Arid/semiarid	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**
Non-200 ecoregions		48,507	65.5	44,265	69.6	37,481	46.7	41,205	54.3	89,286	55.6	87,495	56.0	102,191	53.4	86,676	60.1
Arabian Highlands Woodlands and Shrublands	Yes	6,139	8.3	6,139	9.6	4,105	5.1	6,459	8.5	14,993	9.3	14,993	9.6	15,347	8.0	15,347	10.6
Carnavon Xeric Shrubs	Yes	5,795	7.8	5,795	9.1	3,138	3.9	6,635	8.7	7,630	4.8	7,630	4.9	9,687	5.1	9,687	6.7
Namib-Karoo-Kaokoveld Deserts and Shrublands	Yes	5,700	7.7	225	0.4	-	-	-	-	13,495	8.4	12,895	8.3	-	-	-	-
Atacama-Sechura Deserts	Yes	2,132	2.9	2,132	3.4	2,291	2.9	2,132	2.8	3,036	1.9	3,036	1.9	3,036	1.6	3,036	2.1
Northern Australia and Trans-Fly Savannas	Yes	2,088	2.8	2,088	3.3	5,669	7.1	1,975	2.6	3,187	2.0	3,187	2.0	2,298	1.2	2,298	1.6
Horn of Africa Acacia Savannas	Yes	1,225	1.7	-	-	-	-	-	-	3,475	2.2	-	-	-	-	-	-
Mediterranean Forests, Woodlands and Scrub	Yes	1,172	1.6	1,172	1.8	-	-	-	-	-	-	-	-	200	0.1	200	0.1
Chilean Matorral	Yes	467	0.6	467	0.7	284	0.4	467	0.6	944	0.6	944	0.6	944	0.5	944	0.7
Solomons-Vanuatu-Bismarck Moist Forests		241	0.3	205	0.3	35	0.0	205	0.3	490	0.3	483	0.3	542	0.3	483	0.3
Madagascar Dry Forests		175	0.2	175	0.3	75	0.1	75	0.1	383	0.2	383	0.2	296	0.2	296	0.2
Amazon-Orinoco-Southern Caribbean Mangroves		167	0.2	-	-	186	0.2	-	-	-	-	-	-	301	0.2	-	-
Greater Antillean Moist Forests		150	0.2	823	1.3	617	0.8	823	1.1	322	0.2	1,804	1.2	322	0.2	1,789	1.2
Great Sandy-Tanami-Central Ranges Desert	Yes	118	0.2	118	0.2	36	0.0	-	-	271	0.2	271	0.2	1	0.0	1	0.0
Madagascar Spiny Thicket	Yes	-	-	-	-	75	0.1	75	0.1	-	-	-	-	175	0.1	175	0.1
Rann of Kutch Flooded Grasslands	Yes	-	-	-	-	-	-	-	-	25	0.0	25	0.0	150	0.1	150	0.1
Socotra Island Desert	Yes	-	-	-	-	159	0.2	-	-	-	-	-	-	-	-	-	-
Sonoran-Baja Deserts	Yes	-	-	-	-	15,727	19.6	15,364	20.2	20,825	13.0	20,825	13.3	20,986	11.0	20,986	14.6
Southern Mexican Dry Forests	Yes	-	-	-	-	125	0.2	406	0.5	2,145	1.3	2,145	1.4	1,957	1.0	1,957	1.4
Sudd-Sahelian Flooded Grasslands and Savannas	Yes	-	-	-	-	-	-	-	-	50	0.0	50	0.0	-	-	-	-
Borneo Lowland and Montane Forests		-	-	-	-	-	-	-	-	-	-	-	-	201	0.1	-	-
Greater Antillean Pine Forests		-	-	21	0.0	-	-	21	0.0	-	-	43	0.0	-	-	43	0.0
Greater Sundas Mangroves		-	-	-	-	-	-	-	-	-	-	-	-	88	0.0	-	-
Guinean Moist Forests		-	-	-	-	-	-	-	-	2	0.0	-	-	-	-	-	-
Madagascar Forests and Shrublands		-	-	-	-	23	0.0	23	0.0	42	0.0	42	0.0	23	0.0	23	0.0
Moluccas Moist Forests		-	-	-	-	3,723	4.6	-	-	-	-	-	-	11,637	6.1	-	-
New Guinea Mangroves		-	-	-	-	-	-	-	-	-	-	-	-	818	0.4	-	-

New Guinea Montane Forests	-	-	-	-	-	-	-	-	-	-	-	-	13	0.0	-	-
Nusu Tenggara Dry Forests	-	-	-	-	3,593	4.5	59	0.1	-	-	-	-	2,303	1.2	84	0.1
Southern New Guinea Lowland Forests	-	-	-	-	888	1.1	-	-	-	-	-	-	5,126	2.7	-	-
Sulawesi Moist Forests	-	-	-	-	1,840	2.3	-	-	-	-	-	-	12,582	6.6	-	-
Sumatran Islands Lowland and Montane Forests	-	-	-	-	154	0.2	-	-	-	-	-	-	-	-	-	-
Total	74,075	100.0	63,625	100.0	80,225	100.0	75,925	100.0	160,600	100.0	156,250	100.0	191,225	100.0	144,175	100.0

Chapter 4. Contribution to the authorship

I was in charge of the conception and design of the project; acquisition, analysis, and interpretation of the research data; drafting, analysis, and critical writing of the manuscript.

CHAPTER 4. Freeing agricultural land for future biofuel production in the Neotropics through microalgal cultivation

Diego F. Correa[1, 2*], Hawthorne L. Beyer[2], Hugh P. Possingham[2,4], John García-Ulloa[3], Jaboury Ghazoul[3], Peer M. Schenk[1]

[1]Algae Biotechnology Laboratory, School of Agriculture and Food Sciences, The University of Queensland, Brisbane, QLD 4072, Australia

[2] Centre for Biodiversity and Conservation Science CBCS, The University of Queensland, Brisbane, QLD 4072, Australia

[3] The Nature Conservancy, Arlington, VA 22203, USA

[4] Institute of Terrestrial Ecosystems, ETH Zürich, Universitätstrasse 16, 8092 Zürich, Switzerland

ABSTRACT

Biofuel production is expected to increase in the following decades, particularly in tropical developing countries. The adoption of more sustainable biofuel production alternatives is a necessary step for decreasing greenhouse gas emissions and prevent further biodiversity losses and degradation of native ecosystems. With their high productivity per unit area, and their ability to grow in non-arable lands, microalgal biofuel production systems could become a major sustainable alternative for biofuel production, compared to food crops (i.e., first generation biofuels). However, their potential impacts on biodiversity and carbon storage compared to other biofuel production alternatives, are largely unknown. Through a GIS-based multiple-criteria decision analysis and integer linear programming, we determined best areas for siting microalgal production farms compared with oil palm and sugarcane, aiming at fulfilling 30% of future transport energy demands within four Neotropical countries (Colombia, Ecuador, Panama, and Venezuela), while avoiding areas of high agricultural and biodiversity value. We then compare potential competition with agricultural lands, biodiverse areas, and aboveground biomass for these biofuel production alternatives. Based on our results, microalgal biofuel production is the preferable alternative for reaching a 30% target in future transport energy targets in comparison to oil palm and sugarcane within these Neotropical countries, in terms of reduced land-use change, reduced competition with areas of high biodiversity value, and reduced competition with carbon-rich areas. The reduction of targets in future biofuel blends can decrease potential competition with high-value agricultural lands in the Colombian Caribbean region, and in general, reduce the overall potential environmental impacts of biofuel production. This study can guide decision making towards the identification and adoption of more sustainable biofuel production alternatives within the Neotropical region.

Keywords: Microalgae, oil palm, sugarcane, food crops, biofuel

1. INTRODUCTION

Renewable energy sources will play a prominent role for fulfilling future energy demands and replace fossil fuels (Jacobson and Delucchi 2011, IEA 2017), reducing the negative impacts driven by greenhouse gases (Bellard et al. 2012, Pecl et al. 2017). Among renewable energy sources, biofuels can help in replacing significant amounts of fossil fuels, particularly in the transport sector, which would still need liquid fuels for ships, airplanes and long-haul trucks. In fact, biofuel production could increase from 1.7 to 8.1 million of barrels of oil equivalent day^{-1} between 2016 and 2040, under the implementation of policies that favor the adoption of renewable energy sources for limiting global warming well below 2°C in comparison to pre-industrial levels (IEA 2017), in accordance with the Paris Agreement.

However, a wide arrange of environmental impacts have been related to the production of biofuels (Hill et al. 2006, Fargione et al. 2010, Immerzeel et al. 2014, Correa et al. 2017). These impacts include habitat losses for native species (Koh 2007, Wiens et al. 2011), and increases in greenhouse gas emissions when carbon-rich systems are replaced into monocultures for biofuel production (Fargione et al. 2008, Searchinger et al. 2008, Searchinger et al. 2015). Furthermore, bioenergy production is expected to expand in the biodiverse tropical areas of the world, where vast amounts of undeveloped lands offer higher crop productivities in comparison to temperate regions (Foley et al. 2011, Laurance et al. 2014, Laurance 2015). The combined impacts of a future expansion in biofuel and agricultural production within the tropics can increase competition with food production (Tilman et al. 2009), trigger biodiversity losses and degrade ecosystems and its associated services, including losses in carbon sinks and increases in CO_2 emissions as a result of deforestation (Laurance et al. 2014).

The adoption of alternatives for biofuel production that do not drive direct and indirect land-use changes in agricultural and biodiverse lands, and that reduce greenhouse gas emissions, can increase the sustainability in biofuel production, while reaching growing targets in energy demands. Microalgal biofuel production systems have been proposed as an alternative to first generation biofuels. They do not require fertile soils and thus, in theory, are not expected to directly compete with food production (Schenk et al. 2008, Correa et al. 2017). They can make use of brackish/salt water for their cultivation, avoiding direct competition with freshwater resources (Schenk et al. 2008, Usher et al. 2014), as well as make use of nutrients from wastewater (Abdel-Raouf et al. 2012) and CO_2 from industries (Stephens et al. 2010, Huang and Tan 2014). Furthermore, if culture media is recycled, their grey water footprint (i.e., the volume of polluted water) is expected to be zero, decreasing the overall freshwater use per energy unit compared to terrestrial crops (Gerbens-Leenes 2018). However, their potential impacts on food production, biodiversity, and carbon storage compared to other biofuel production alternatives, are largely unknown.

The Neotropical region harbor several of the most important areas for biodiversity conservation globally, as a result of its high number of total, endemic, and threatened species (Gentry 1982, Rull 2011), as well as the presence of systems with high ecological importance (e.g., the Amazon rainforest) (Myers et al. 2000, Foley et al. 2007, Watson et al. 2018). Additionally, future biofuel and agricultural expansion are likely to occur in the region as it has large areas of underexploited lands that are suitable for biofuel and food production (Butler and Laurance 2009, Laurance et al. 2014).

Here, we aim at understanding the potential direct competition of three different alternatives of biofuel production (i.e., microalgae, oil palm, and sugarcane) with areas of high agricultural and biodiversity value, and with carbon-rich areas, for fulfilling a 30% target in transport energy demands by 2050 within four Neotropical countries (i.e., Panama, Colombia, Ecuador, and Venezuela). Currently, oil palm is considered the most productive food crop for biodiesel production, and sugarcane the most productive food crop for bioethanol production in the region. The assessment of these potential conflicts can guide decision making towards the implementation of more sustainable biofuel production alternatives in future development scenarios.

2. METHODS

Our analyses were developed in four Neotropical countries (Panama, Colombia, Ecuador, and Venezuela), which are among the most biodiverse on Earth as a result of their complex biogeographical history and their wide range of climatic conditions within the tropical region (Gentry 1982, Rull 2011). For each biofuel feedstock (i.e., microalgae, oil palm, and sugarcane), we developed a model based on integer linear programming (Beyer et al. 2016) for determining best production areas to satisfy a 30% target in internal energy demands, while avoiding areas of high agricultural and biodiversity value. The model was developed using the software R and Gurobi optimizer, based on the following formula (Correa et al. 2019):

$$\text{maximize} \sum_i P_i^2 \, x_i / \left(\text{maximum}(A_i, B_i) + 1\right)$$

subject to

$$\sum_i D_i \, x_i = T$$

$$0 \leq x_i \leq 0.8$$

Where i corresponds to each pixel, P corresponds to the microalgal profitability layer (ranging from 0 to 1), "maximum" corresponds to the maximum value among agricultural value A (ranging from 0 to 1) and biodiversity value B (ranging from 0 to 1), x corresponds to the decision variable given by the software (ranging from 0 to 0.8 for microalgae, and from 0 to 0.9 for oil palm and sugarcane), D represents the productivity values in units of energy by 2050 (GJ pixel^{-1} year^{-1}) (See Supplementary Information for details), and T represents 30% of each country's transport energy demands by 2050 (GJ year^{-1}). Squaring the profitability in the numerator and using the maximum value among A or B in the denominator ensures that pixels with lower or average profitabilities or with either high agricultural or high biodiversity values are excluded from final solutions. Within each pixel, the percentage of available area for microalgal cultivation ranged from 0 to 0.8, assuming that 20% would include associated infrastructure (Wigmosta et al. 2011). For oil palm and sugarcane, which can be more densely produced, the percentage of available area cultivation ranged from 0 to 0.9. The percentage of available area for cultivation was calculated after excluding water bodies (Lehner and Döll 2004), protected areas (UNEP-WCMC 2016), Key Biodiversity Areas (KBA) (BirdLife International 2016), and urban areas (Schneider et al. 2009).

For each cultivation feedstock, the profitability layer was obtained through a GIS-based multiple-criteria decision analysis (MCDA) developed in the software ArcGIS 10.5, at a spatial resolution of 5 × 5 km. For microalgae, two cultivation scenarios were considered. Scenario 1: Cultivation by using fresh/brackish/salt water sources, and Scenario 2: Cultivation by using seawater, which does not compete with freshwater (i.e., assuming that microalgal strains tolerant to a wide range of salinity conditions are cultivated, thereby preventing the use of freshwater for maintaining salinity as water evaporates) (Borowitzka and Moheimani 2013). For microalgal production, the profitability layer was the result of overlaying water availability, microalgal lipid productivity, availability of flat lands, and proximity to main transport networks (i.e., main roads and railroads). For Scenario 1 water availability included the proximity to rivers, irrigation dams and fresh/brackish/salt groundwater sources after taking into account water depletion within watersheds (Brauman et al. 2016), along with the aridity index (i.e., the availability of water from precipitation in relation to potential evapotranspiration) (Trabucco and Zomer 2009) and proximity to seawater. For Scenario 2 water availability corresponded to proximity to seawater. Water availability is essential for microalgal cultivation (Chisti 2007, Schenk et al. 2008), while high microalgal lipid productivities (Slade and Bauen 2013) and flat lands reduce production costs (Wigmosta et al. 2011), and the proximity to main transport networks facilitates access to fertilizers and markets (Venteris et al. 2014, Slegers et al. 2015). Future potential mean annual precipitation, mean annual potential evapotranspiration, and mean annual temperature, which affect the aridity index and lipid productivities, were calculated by 2050 (Chapter 3), based on an ensemble model for the climate change Representative Concentration Pathway (RCP) 8.5 (i.e., high-emissions climate change scenario) (Riahi et al. 2011). This ensemble model was constructed by averaging mean annual and monthly temperatures, minimum monthly temperatures, maximum monthly temperatures, and mean annual precipitation values among the following General Circulation Models (GCMs) BCC-CSM1-1, CCSM4, GISS-E2-R, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM-CHEM, MRI-CGCM3, and NorESM1-M (Hijmans et al. 2005). The layers were overlayed by using fuzzy membership functions and the AND/OR Boolean operators, in which memberships are assigned without the use of weights (Raines et al. 2010) (See Supplementary Information for details).

For oil palm and sugarcane, the profitability layer was the result of overlaying water availability, agro-climatically attainable yield in dry weight by 2050 (IIASA/FAO 2012), the availability of flat lands, the proximity to main transport networks (i.e., main roads and railroads), and the proximity to current cultivation areas (You et al. 2014, Furumo and Aide 2017). Water availability included the proximity to rivers, irrigation dams, and fresh groundwater sources after taking into account water depletion within watersheds (Brauman et al. 2016), along with the aridity index (Trabucco and Zomer 2009). While freshwater availability is necessary for oil palm and sugarcane cultivation (Adzemi 2014, FAO 2018), high agro-climatically attainable yields and flat lands (which favour farming intensification) increase profitability (Garnett et al. 2013), the proximity to main transport networks facilitates access to fertilizers and markets (Laurance et al. 2014), and the proximity to current plantations facilitates the establishment of new cultivation areas (Garcia-Ulloa et al. 2012). For both oil palm and sugarcane, we obtained the agro-climatically attainable yields by 2050 from the Global Agro-Ecological Zones GAEZ database (IIASA/FAO 2012) by averaging the yields among the following climate change models for 2050: CCCma CGCM2 A2, CSIRO Mk2 A2, Hadley CM3 A2, and MPI ECHAM4 A2, which are comparable with the high-emissions RCP 8.5 scenario used for future microalgal cultivation (Riahi et al. 2011). We selected the layers corresponding to irrigated and high-input level (i.e., assuming that freshwater can be readily obtained for crop cultivation and that a high level of intensification for crop production will be achieved).

The agricultural value corresponded to the potential annual gross economic rents from agricultural lands, after rescaling from 0 to 1 by using a linear membership function with a maximum input value of 800 USD ha^{-1}, which corresponds to highly profitable lands (Naidoo and Iwamura 2007). Biodiversity value was the result of overlaying the number of vertebrate species, the number of threatened vertebrate species, the number of vertebrate species with small distribution ranges (Jenkins et al. 2013), the presence of areas with low human pressures (Venter et al. 2016), the presence of islands (which contain more endemic populations/species compared to mainlands) (Kier et al. 2009, Tershy et al. 2015, McCreless et al. 2016), and the percentage of mangroves within each pixel (i.e., 25 km^2) (Giri et al. 2011), after rescaling from 0 to 1 by using linear membership functions.

Future transport energy demands were calculated for each country based on current transport energy demands (IEA 2018) and an estimated annual increase in transport energy consumption at 2.5% for non-OECD Americas (EIA 2016). We determined land-covers potentially replaced by microalgae, oil palm, and sugarcane (Channan et al. 2014). Non-parametric Dunn's tests with Bonferroni corrections (Dino 2017) were performed to detect statistically significant differences among biofuel production alternatives per country, in relation to agricultural and biodiversity values, and aboveground biomass. Potential conflicts among each biofuel production alternative, agricultural value, biodiversity value, and aboveground biomass, were mapped.

3. RESULTS

For fulfilling 30% of each country's transport energy demands by 2050, best areas for microalgal biofuel production at lowest direct competition with high-value agricultural lands and biodiversity, would mainly correspond to dry lowlands (Fig. 1). For Scenarios 1 (use of fresh/brackish/salt water) and 2 (use of seawater), main cultivation areas would be located in the Colombian Caribbean region (i.e., mostly in the Guajira desert and around the San Jacinto mountains) and interandean Valleys (i.e., mainly in the Alto Magdalena Valley), in the Ecuadorian coastal region (i.e., mainly in provinces of Santa Elena, Manabí, and Guayas), in the Panamanian Pacific coast (i.e., mainly in the provinces of Veraguas and Coclé), and in the Venezuelan Caribbean coastline (i.e., around the Gulf of Venezuela in the state of Falcón and around the Lake Maracaibo in the state of Zulia). Based on these cultivation scenarios, potential replaced land-covers would correspond to cropland/natural vegetation mosaics (24.9–28.5%), followed by savannas (19.5–20.5%), grasslands (10.5–10.8%), croplands (10.6–13.1%), open shrublands (7.7–7.9%), and woody savannas (7.1–7.3%) (Table 1).

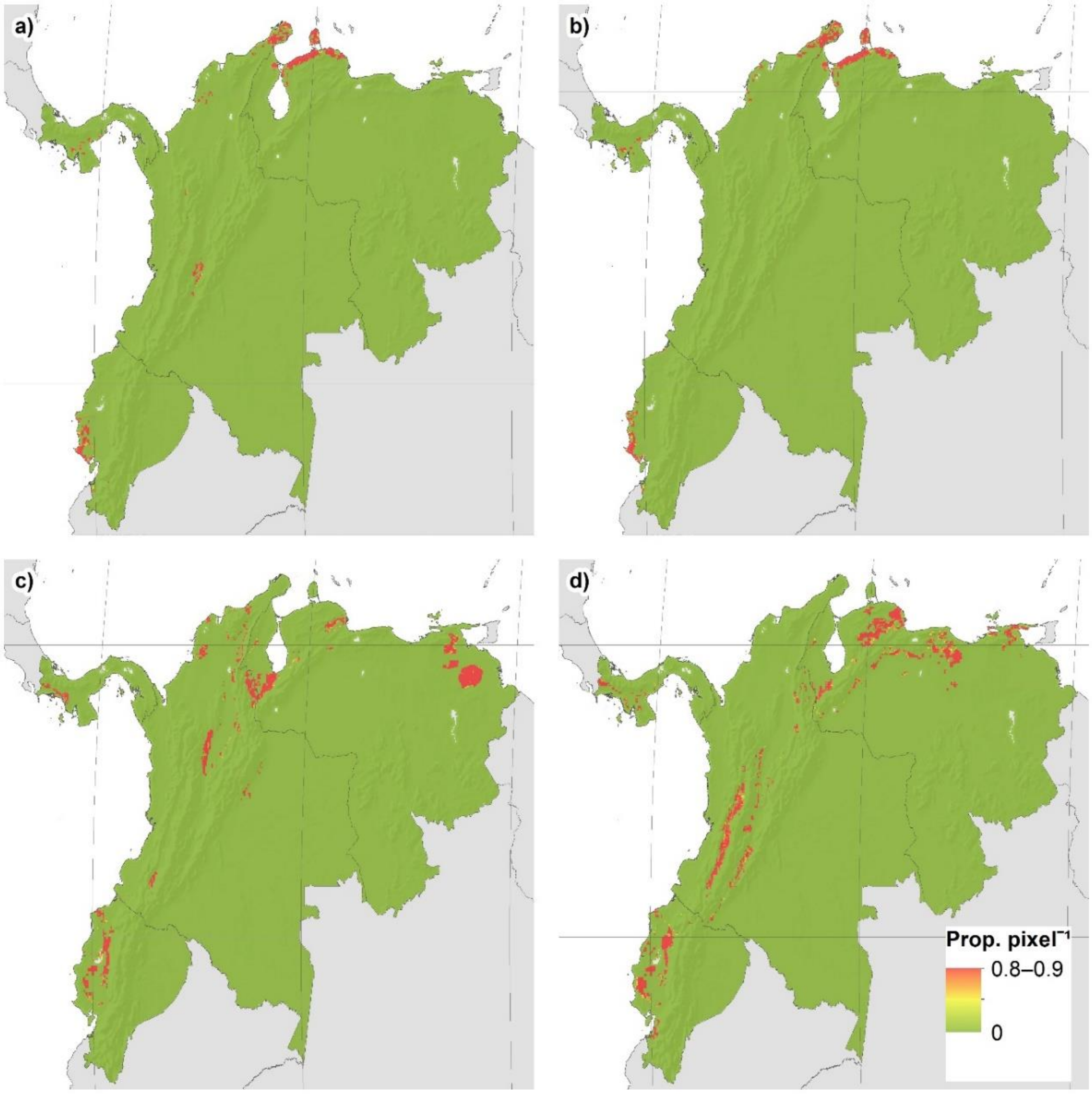

Figure 1. Production areas for fulfilling each country's 30% transport energy demands by 2050 based on: a) microalgae (i.e., use of fresh/brackish/salt water), b) microalgae (i.e., use of seawater), c) oil palm, and d) sugarcane. The maximum proportion (Prop.) of cultivation area per pixel corresponds to 0.8 for microalgae and 0.9 for oil palm and sugarcane.

Table 1. Land covers potentially replaced for fulfilling 30% of transport energy demands by 2050 in four Neotropical countries (Colombia, Ecuador, Panama, Venezuela)by using microalgae, oil palm, and sugarcane. Land covers were obtained from the MODIS derived global mosaic for 2012 at a resolution of 5 arcminutes (Channan et al. 2014). Microalgal cultivation scenario 1: use of fresh, brackish and saltwater sources; microalgal cultivation scenario 2: use of seawater.

	Scenario 1 (microalgae)		**Scenario 2 (microalgae)**		**Oil palm**		**Sugarcane**	
Land Cover	**Area (km^2)**	**Area (%)**	**Area (km^2)**	**Area (%)**	**Area (km^2)**	**Area (%)**	**Area (km^2)**	**Area (%)**
Cropland/Natural vegetation mosaic	6,837.2	28.5	5,994.7	24.9	17,686.9	35.0	25,687.5	35.6
Savannas	4,929.2	20.5	4,683.7	19.5	10,038.8	19.9	13,169.5	18.3
Grasslands	2,582.6	10.8	2,518.6	10.5	97.8	0.2	1,712.5	2.4
Croplands	2,543.1	10.6	3,159.3	13.1	2,912.8	5.8	1,823.0	2.5
Open shrublands	1,842.1	7.7	1,888.4	7.9	890.6	1.8	5,492.1	7.6
Woody savannas	1,710.7	7.1	1,753.8	7.3		0.0		0.0
Evergreen Broadleaf forest	1,034.9	4.3	1,267.2	5.3	16,373.1	32.4	22,017.2	30.5
Deciduous Broadleaf forest	110.8	0.5		0.0	190.1	0.4		0.0
Others	2,409.5	10.0	2,784.1	11.6	2,334.9	4.6	2,173.1	3.0
Total	24,000.0	100.0	24,050.0	100.0	50,525.0	100.0	72,075.0	100.0

Areas for oil palm production at lowest direct competition with high-value agricultural lands and biodiversity, would be mainly spread along humid lowlands in the Colombian Caribbean and Catatumbo regions and Middle Magdalena Valley, the Ecuadorian Pacific lowlands (i.e., mainly in the provinces of Esmeraldas, Pichincha, Manabí, Los Ríos, and Guayas), the Panamanian Pacific coast (i.e., mainly in the provinces of Chiriquí and Veraguas), and the Venezuelan northern lowlands (i.e., mainly the states of Zulia, Táchira, Monagas, and Delta Amacuro). Areas for sugarcane production at lowest direct competition with high-value agricultural lands and biodiversity would be located in valleys and foothills along mountain ranges, mainly in the Colombian Cauca and Magdalena Valleys, the Ecuadorian Pacific lowlands (i.e., mainly in the provinces of Pichincha, Los Ríos, Manabí, and Guayas), the Panamanian Pacific coast (i.e., mainly in the provinces of Chiriquí and Veraguas), and the Venezuelan northern lowlands (i.e., mainly in the states of Lara, Falcón, Guárico, and Sucre). Land-covers potentially replaced by oil palm and sugarcane include cropland/natural vegetation mosaics (35 and 35.6% for oil palm and sugarcane, respectively), followed by evergreen broadleaf forests (32.4 and 30.5% for oil palm and sugarcane, respectively), and savannas (19.9 and 18.3% for oil palm and sugarcane, respectively).

Microalgal cultivation would lead to lower competition with high-value agricultural lands in Ecuador (compared to sugarcane) and Venezuela (compared to oil palm and sugarcane) (Fig. 2). Microalgal cultivation would lead to lower competition with biodiverse and carbon-rich areas, except for biodiversity in Colombia compared to sugarcane (Figs. 3, 4).

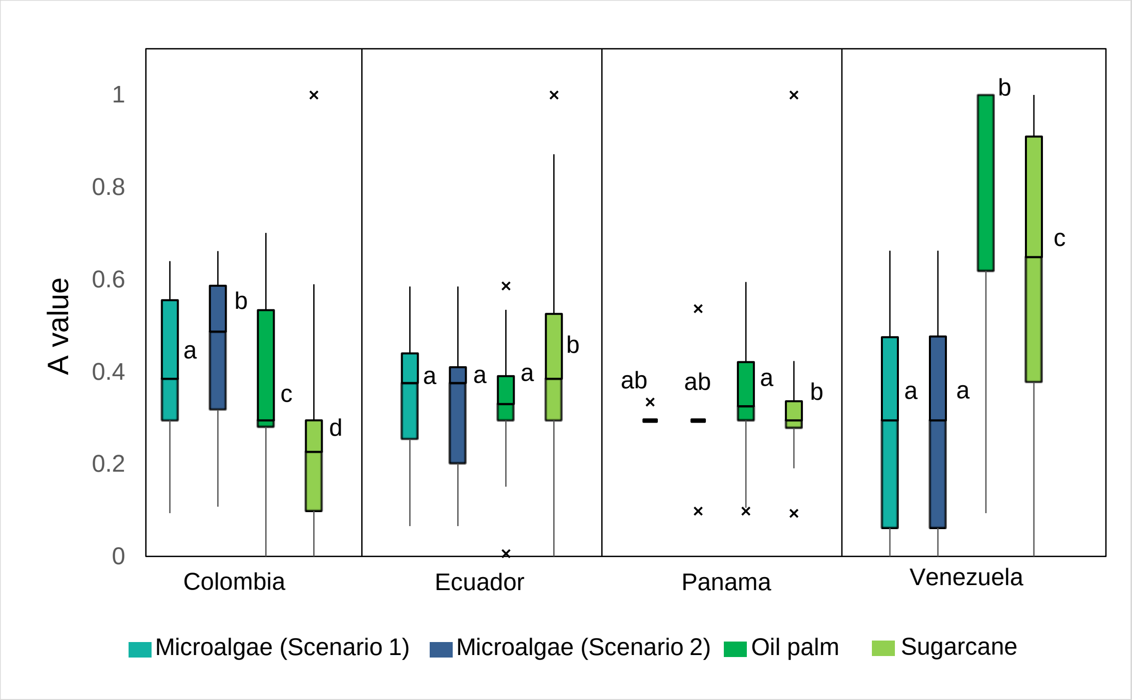

Figure 2. Boxplots showing statistically significant differences among biofuel production alternatives (microalgae, oil palm, sugarcane) in relation to the agricultural (A) value of lands needed for fulfilling each country's 30% of transport energy demands in 2050. Letters represent homogeneous groups based on post hoc Dunn's tests with Bonferroni corrections. Asterisks represent the maximum and minimum outliers (defined after multiplying the interquartile range by 1.5). Microalgal cultivation scenario 1 (use of fresh, brackish and saltwater sources), microalgal cultivation scenario 2 (use of seawater).

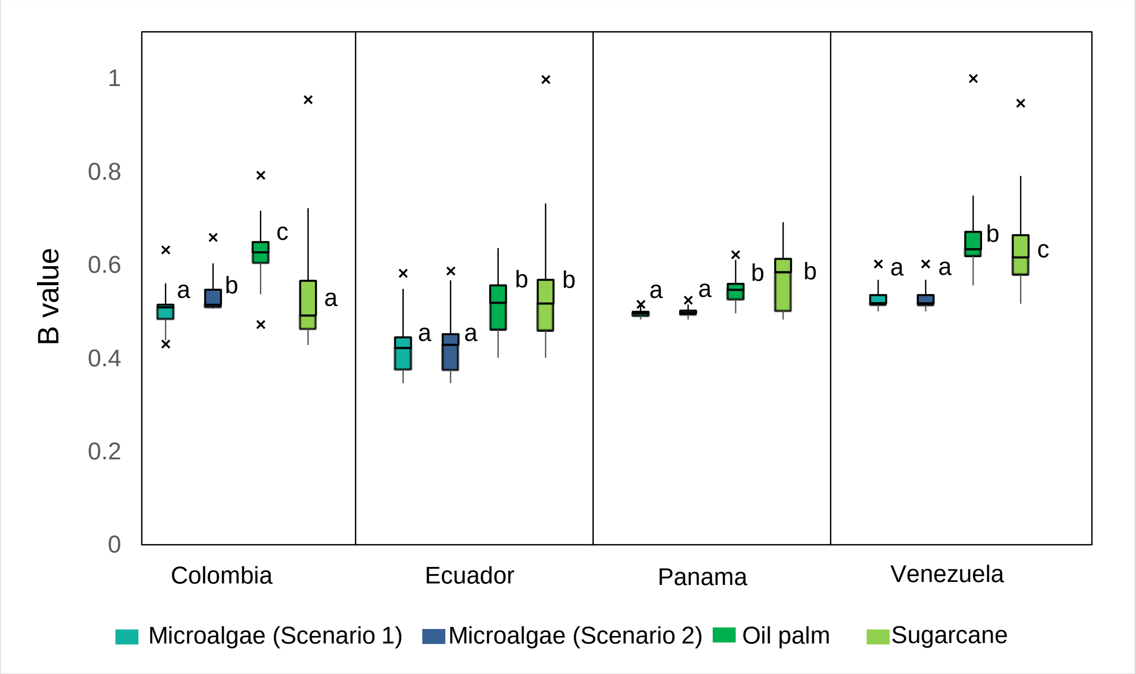

Figure 3. Boxplots showing statistically significant differences among biofuel production alternatives (microalgae, oil palm, sugarcane) in relation to the biodiversity (B) value of lands needed for fulfilling each country's 30% of transport energy demands in 2050. Letters represent homogeneous groups based on post hoc Dunn's tests with Bonferroni corrections. Asterisks represent the maximum and minimum outliers (defined after multiplying the interquartile range by 1.5). Microalgal cultivation scenario 1 (use of fresh, brackish and saltwater sources), microalgal cultivation scenario 2 (use of seawater).

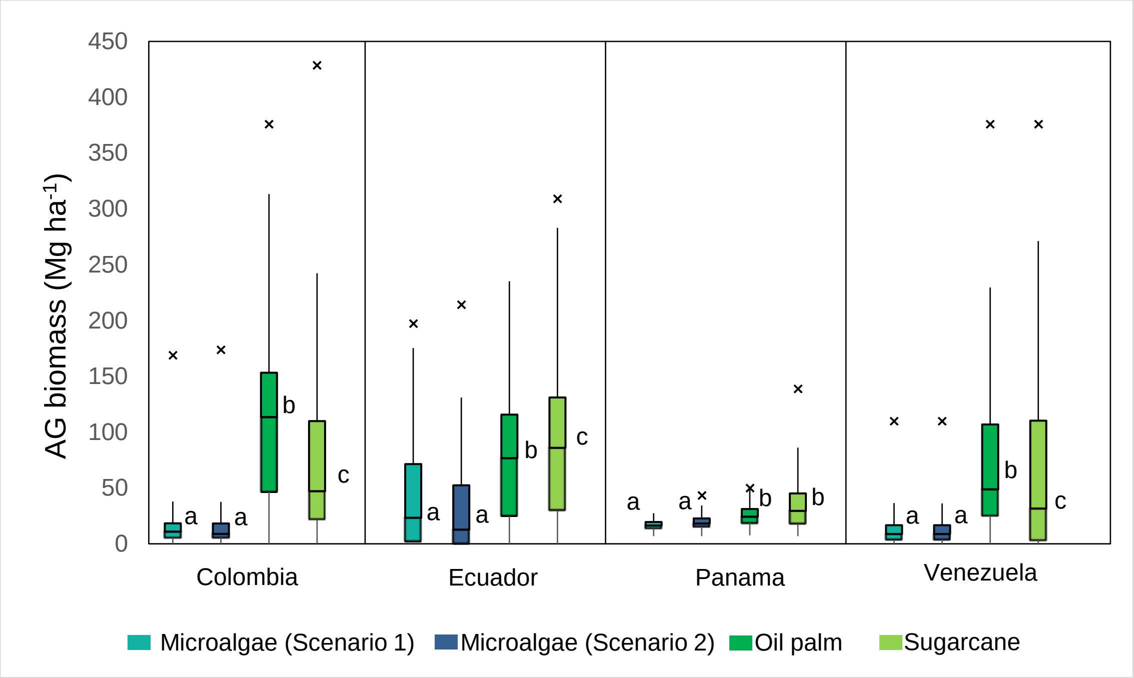

Figure 4. Boxplots showing statistically significant differences among biofuel production alternatives (microalgae, oil palm, sugarcane) in relation to the aboveground (AG) biomass of lands needed for fulfilling each country's 30% of transport energy demands in 2050. Letters represent homogeneous groups based on post hoc Dunn's tests with Bonferroni corrections. Asterisks represent the maximum and minimum outliers (defined after multiplying the interquartile range by 1.5). Microalgal cultivation scenario 1 (use of fresh, brackish and saltwater sources), microalgal cultivation scenario 2 (use of seawater).

Higher targets in biofuel demands would increase competition with areas of higher agricultural and biodiversity value and larger aboveground biomass (Figs. 5, 6, 7).

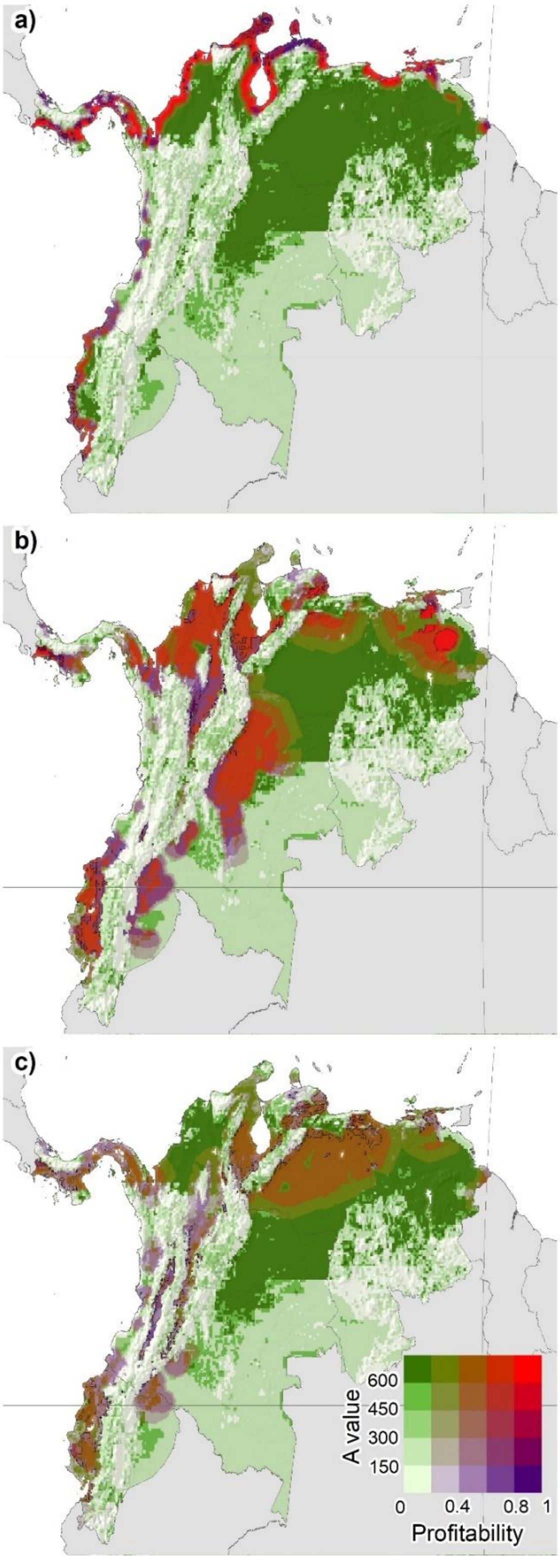

Figure 5. Overlapping between profitability and agricultural value (A value in USD ha^{-1}*) for (a) microalgal cultivation scenario 2: use of seawater, (b) oil palm, and (c) sugarcane. Purple colors show areas with high potential profitabilities and low potential conflicts with food production, while red show areas with high potential profitabilities and high potential conflicts with food production. Cultivation areas for fulfilling each country's 30% transport energy demands by 2050 are delineated in black.*

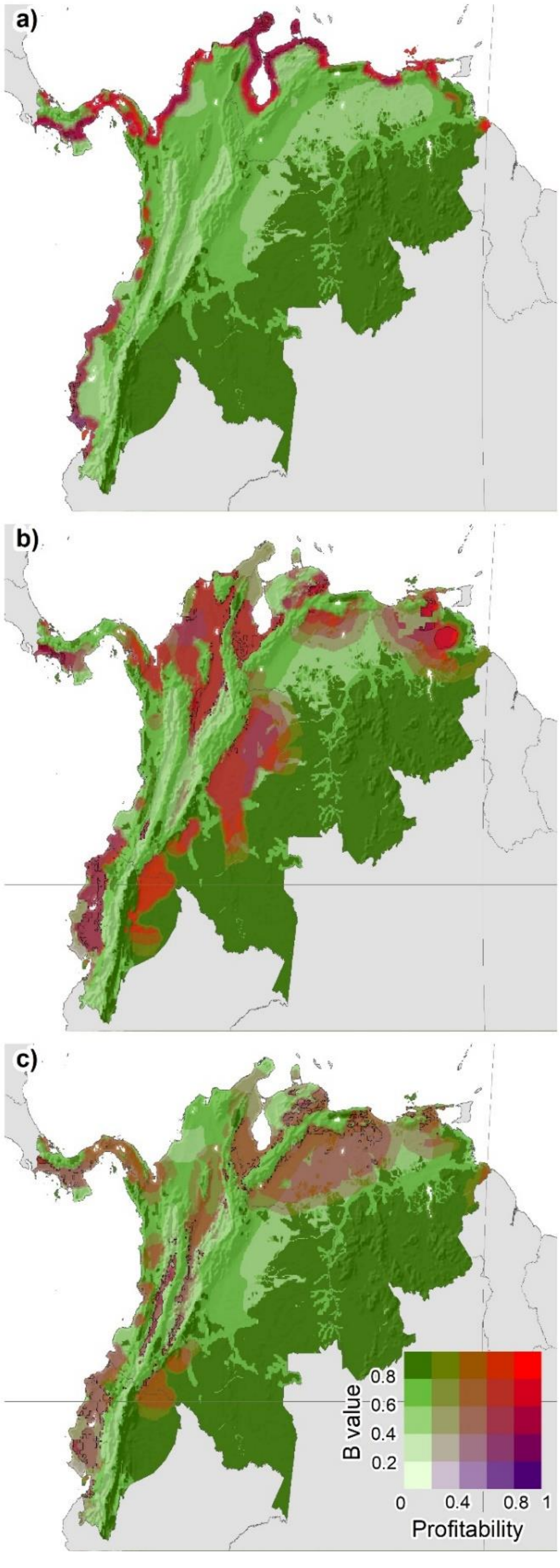

Figure 6. Overlapping between profitability and biodiversity value (B value ranging from 0 to 1) for (a) microalgal cultivation scenario 2: use of seawater, (b) oil palm, and (c) sugarcane. Purple colors show areas with high potential profitabilities and low potential conflicts with biodiversity, while red show areas with high potential profitabilities and high potential conflicts with biodiversity. Cultivation areas for fulfilling each country's 30% transport energy demands by 2050 are delineated in black.

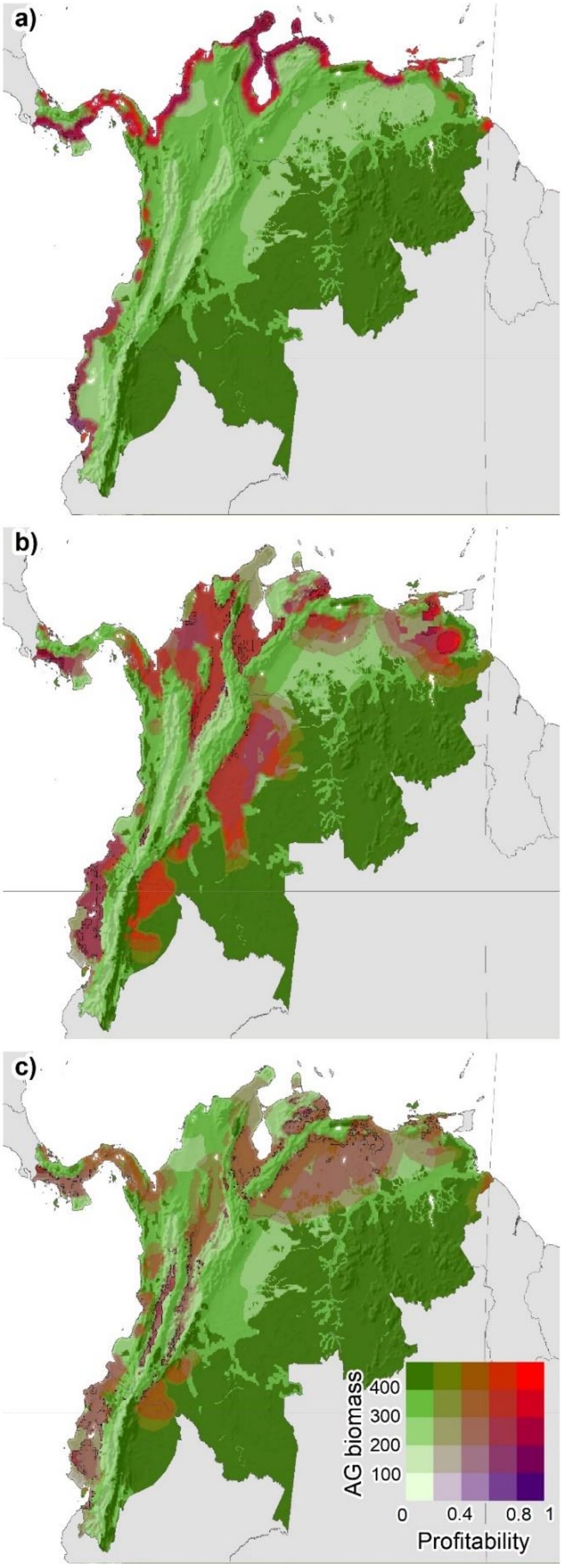

Figure 7. Overlapping between profitability and aboveground biomass (AG biomass in tonne ha^{-1}*) for (a) microalgal cultivation scenario 2: use of seawater, (b) oil palm, and (c) sugarcane. Purple colors show areas with high potential profitabilities and low potential conflicts with carbon storage, while red show areas with high potential profitabilities and high potential conflicts with carbon storage. Cultivation areas for fulfilling each country's 30% transport energy demands by 2050 are delineated in black.*

4. DISCUSSION

Future biofuel production levels will likely increase in the Neotropics, potentially impacting food production, biodiversity, and carbon storage in the region. However, the environmental impacts of main biofuel production systems (i.e., oil palm and sugarcane) and promising biofuel production alternatives (i.e., microalgae), based on future targets in transport energy demands, have not been evaluated in the region.

Our results show that in Colombia, Ecuador, Panama, and Venezuela, microalgal biofuel production would need between 48 and 33% the land required by oil palm and sugarcane, respectively, for fulfilling the same levels of future transport energy demands. This is explained by the higher microalgal biofuel production efficiencies per unit area, compared to any other biofuel crop (Chisti 2008, Correa et al. 2017). Our model considered maximum attainable yields for oil palm and sugarcane, based on optimal cultivation techniques (i.e., high-input cultivation under irrigation) (IIASA/FAO 2012), but conservative yield estimates for microalgae. Based on biodiesel production, future microalgal lipid productivities could reach a six-fold increase in the study region (Chisti 2007) compared to current estimations (i.e., from maximum attainable oil yields of 22,800 to 136,900 L ha^{-1}) (Moody et al. 2014), as a result of technological improvements (e.g., use of photobioreactors) and cultivation of more productive microalgae strains (e.g., through the selection and cultivation of microalgae with higher lipid contents per cell). Thus, even under expected future higher productivities for oil palm and sugarcane (Murphy 2009, Marin et al. 2016), the relative advantage of microalgae in terms of reduced land-use is expected to increase.

At a global scale, microalgal biomass and lipid productivities, which increase biofuel production levels, are proportional to solar irradiance and mean annual temperature (Lundquist et al. 2010, Moody et al. 2014, Venteris et al. 2014). Microalgal strains can be further selected to thrive under higher temperature conditions. Thus, based on a Representative Concentration Pathway (RCP) 8.5 climate change scenario (i.e., a high-emissions climate change scenario) (Riahi et al. 2011), microalgal profitability would be highest in lowlands within the study region. In contrast, more restricted temperature ranges for the optimal cultivation of oil palm and sugarcane, coupled with changes in precipitation and evapotranspiration patterns as a result of global warming, would inevitably alter future optimal cultivation areas, unless new varieties tolerant to higher temperatures and drought are developed (de Carvalho et al. 2015, Paterson et al. 2015, Zhao and Li 2015). Based on the Global Agro-Ecological Zones model (IIASA/FAO 2012), maximum oil palm and sugarcane attainable yields would be found at higher altitudes compared to current cultivation areas, increasing the cultivation suitability in interandean valleys and higher-altitude foothills for oil palm and sugarcane, respectively.

Based on our model, which aims to increase profitability in biofuel production while reducing direct competition with high-value agricultural areas and important for biodiversity conservation, microalgal cultivation would mainly overlap dry lowlands within countries (i.e., areas with median annual precipitation values equal to 547 and 498 mm for the microalgal cultivation scenarios 1 and 2, respectively, which correspond to semi-arid lands), with more than 83% of production areas potentially replacing cropland/natural vegetation mosaics, savannas, grasslands, croplands, open shrublands, and woody savannas. In contrast, even after reducing competition with high-value agricultural lands and with biodiverse areas, oil palm and sugarcane cultivation would overlap more humid regions (i.e., areas with median precipitation values equal to 1,607 and 1,382 mm for oil palm and sugarcane, respectively) and potentially replace a higher proportion of evergreen broadleaf forests (i.e., 32.4 and 30.5% of total production areas for or oil palm and sugarcane, respectively). These broadleaf forests harbor high biodiversity values and hold higher amounts of aboveground biomass compared to grasslands, croplands, and open shrublands (Avitabile et al. 2016). Thus, microalgal cultivation would lead to a lower competition with biodiverse and carbon-rich areas within countries, compared to oil palm and sugarcane (with the exception of microalgae and sugarcane in Colombia for biodiversity).

Although in the study region recent oil palm and sugarcane plantations have mostly replaced non-forested areas (Furumo and Aide 2017, Rueda Ordoñez et al. 2018), reaching biofuel blends for the increasing future transport energy demands (which has not been considered by previous studies) would likely increase deforestation. Zoning oil palm and sugarcane cultivation to areas of lower biodiversity value, such as pastures, transformed and degraded lands (Garcia-Ulloa et al. 2012, Castiblanco et al. 2013, Ocampo-Peñuela et al. 2018, Rueda Ordoñez et al. 2018), may be an option for reducing direct conflicts with forested regions, however at an expense of biofuel productivity per unit area, unless targets in biofuel production are reduced.

The potential impact of microalgal cultivation on agricultural lands does not follow a consistent pattern among countries. Microalgal cultivation in Ecuador (compared to sugarcane) and Venezuela (compared to oil palm and sugarcane) would lead to lower competition with high-value agricultural lands. In contrast, microalgal cultivation in Colombia would likely overlap areas of higher agricultural value compared to oil palm and sugarcane. This results from the high profitability of agricultural lands estimated for the Colombian Caribbean region (i.e., higher than 800 USD ha^{-1} for most lands outside La Guajira department) (Naidoo and Iwamura 2007). This competition would be highest when using seawater for microalgal cultivation, which shows a trade-off between agricultural value and seawater use in the Colombian Caribbean.

As expected, higher competition with food production, biodiversity, and carbon storage would occur if fulfilling higher targets in transport energy demands, either for internal consumption or if biofuels become an export commodity, as pixels with lower profitabilities and higher agricultural, biodiversity, and aboveground biomass values are added into final solutions. Thus, increasing mandates in biofuel blends (e.g., current bioethanol and biodiesel are mandated at 10% in Colombia) based on cultivation of feedstocks within each country, or developing a market for their exportation, would likely increase impacts on agricultural production, biodiversity, and ecosystems services (e.g., carbon storage and water provision) in the study region.

A careful planification of future agricultural development in the Neotropical region, based on explicit targets in food and energy demands, coupled with goals for reducing biodiversity losses and maintaining ecosystem services (e.g., carbon storage and freshwater provision) should help in evaluating potential environmental impacts of biofuel production alternatives. Further analyses based on the availability of nutrients (i.e., considering fertilizers or wastewater sources), CO_2 sources (i.e., based on industrial and agricultural sources including anaerobic digesters), and freshwater, can improve the understanding on the overall environmental impacts of biofuel production alternatives within the Neotropical region. While technological improvements increase the cost-effectiveness of microalgal production systems—for instance, through the obtention of free nutrients and CO_2 (Slade and Bauen 2013), or through the development of biorefinery systems that produce biofuels (González-González et al. 2018) along with food or animal feed (Rösch et al. 2018)—governments can support more sustainable biofuel production alternatives based on their relative environmental benefits (Correa et al. 2019). Furthermore, microalgal production systems could be co-located with current oil palm and sugarcane production systems (Moreno-Garcia et al. 2017, Klein et al. 2018), aiming at reducing land footprint and increase the sustainability of current biofuel production systems.

5. CONCLUSIONS

Considering potential conflicts among biofuel production, food production, biodiversity, and carbon storage is fundamental for improving decision making towards the identification and adoption of more sustainable biofuel production systems. Within the Neotropical region, one of the most diverse in the world and with high potential for future agricultural development, the implementation of microalgal biofuel production systems would lead to lower direct competition with areas of high biodiversity and carbon storage. For reaching 30% of future transport energy demands, potential competition with high-value agricultural lands would likely occur for microalgal production systems in Colombia, being highest when using seawater for microalgal cultivation as a result of high-value agricultural lands in the Caribbean region. Overall, the availability of dry lowlands in relation to domestic transport energy demands would favor the siting of microalgal production systems at lower direct competition with biodiversity and aboveground carbon sinks. However, potential conflicts with dry ecosystems are likely to emerge.

Chapter 4. Supplementary Information

1. Construction of profitability layers

Using ArcGIS 10.5, a GIS-based multiple-criteria decision analysis (MCDA) was developed for constructing each profitability layer (i.e., ranging from 0 to 1), for the cultivation of microalgae, oil palm, and sugarcane at a spatial resolution of 5 × 5 km. For constructing these profitability layers, several suitability layers (Figs. S1, S2, S3, and S4) were overlaid using the AND/OR Boolean operators, which retrieve the likelihood of belonging to any suitability layer based without the use of weights. Each suitability layer was constructed through the use of linear and sigmoid membership functions (i.e., applying fuzzy logic) (Raines et al. 2010). Linear memberships were assigned based on the following formula:

$$\mu(x) = 0 \; if \; x < min, \mu(x) = 1 \; if \; x > max$$

$$otherwise \; \mu(x) = \frac{(x - min)}{(max - min)}$$

Where *x* corresponds to each pixel value, *max* corresponds to the maximum value among pixels, and *min* corresponds to the minimum value among pixels.

Sigmoid large memberships (i.e., large inputs have large memberships) were assigned based in the following formula:

$$\mu(x) = \frac{1}{1 + \frac{x}{f_2}^{-f_1}}$$

And sigmoid small memberships (i.e., small inputs have small memberships) were assigned based in the following formula:

$$\mu(x) = \frac{1}{1 + \frac{x}{f_2}^{f_1}}$$

Where f_1 is the spread of the function (defined as 5) and f_2 is the midpoint. The midpoints (Table S1), are assigned a membership value of 0.5.

The profitability layer for microalgal cultivation was constructed by overlaying water availability (i.e., fresh/brackish/salt water availability for Scenario 1, proximity to oceans for Scenario 2), lipid productivity, availability of flat lands, and proximity to transport networks (i.e., main roads and railroads) (Figs. S1, S2), through the AND Boolean operator. The profitability layers for oil palm and sugarcane were constructed by overlaying water availability, agro-climatically attainable yield, availability of flat lands, proximity to main transport networks (i.e., main roads and railroads), and proximity to current cultivation areas (You et al. 2014, Furumo and Aide 2017) (Figs. S3, S4), through the AND Boolean operator.

For the microalgal cultivation scenario 1, water availability excluding oceans after taking into account water depletion was overlaid with the aridity index and with the proximity to oceans, using the OR Boolean operator. Water availability excluding oceans was overlaid with water depletion driven by human activities (Brauman et al. 2016), using the AND Boolean operator. The water depletion layer was obtained by rescaling the original water depletion percentages within watersheds obtained by Brauman et al. (2016) into suitability values ranging from 0 to 1 (Table S2). Water availability excluding oceans resulted from overlaying the proximity to rivers, proximity to irrigation dams, and proximity to fresh/brackish/salt groundwater sources, using the OR Boolean operator. The proximity to rivers, irrigation dams, fresh/brackish/salt groundwater sources, oceans, and transport networks was based on the use of a cost layer (i.e., cost distance), in which the slope was rescaled through a linear function into 1 to 10 to account for access restrictions these due to rugged terrain (Correa et al. 2019).

For oil palm and sugarcane cultivation, freshwater availability after taking into account water depletion was overlaid with the aridity index, using the OR Boolean operator. Freshwater availability was overlaid with water depletion driven by human activities (Brauman et al. 2016) (Table S2), using the AND Boolean operator. Freshwater availability resulted from overlaying the proximity to rivers, proximity to irrigation dams, and proximity to fresh groundwater sources, using the OR Boolean operator, and considering a cost distance based on slope.

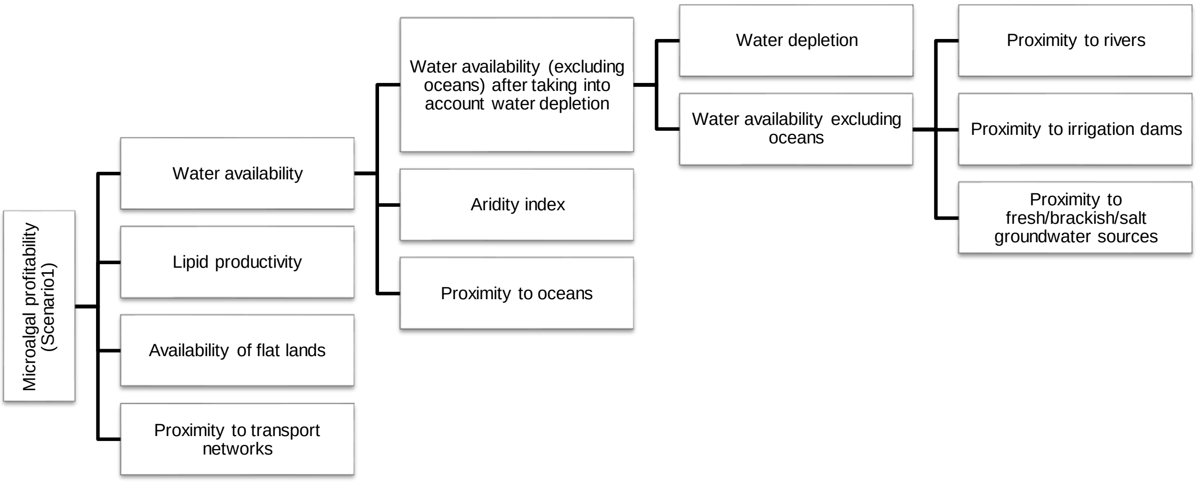

Figure S1. Overlaying of suitability layers for the development of a profitability model for siting biodiesel production microalgal farms by 2050. Scenario 1: Use of fresh, brackish, or salt water.

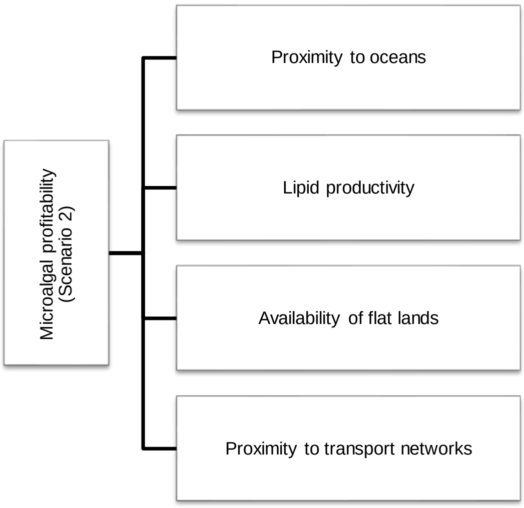

Figure S2. Overlaying of suitability layers for the development of a profitability model for siting biodiesel production microalgal farms by 2050. Scenario 2: Use of seawater.

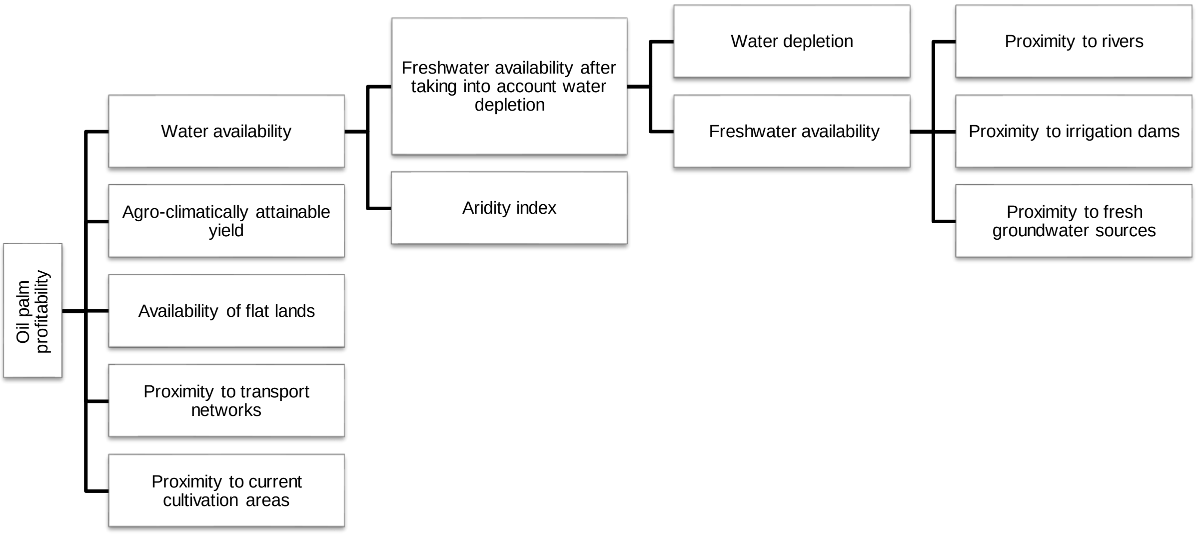

Figure S3. Overlaying of suitability layers for the development of a profitability model for oil palm cultivation by 2050.

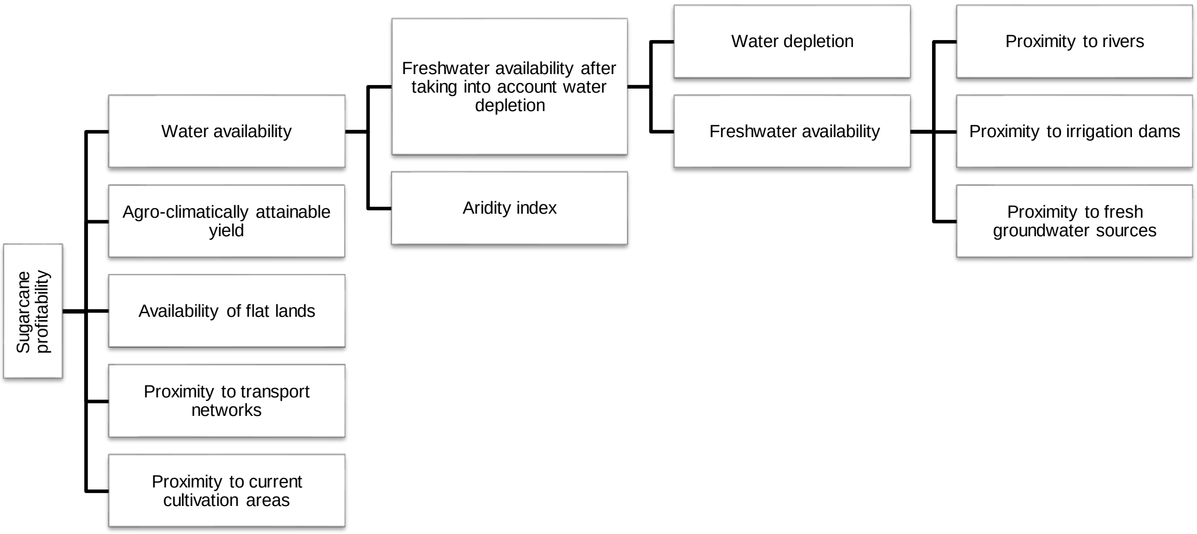

Figure S4. Overlaying of suitability layers for the development of a profitability model for sugarcane cultivation by 2050.

1.1 Biodiversity value

Biodiversity value resulted from overlaying the number of vertebrate species, the number of threatened vertebrate species, the number of vertebrate species with small distribution ranges (Jenkins et al. 2013), the presence of areas with low human pressures (Venter et al. 2016), the presence of islands (which contain more endemic populations/species compared to mainlands) (Kier et al. 2009, Tershy et al. 2015, McCreless et al. 2016), and the percentage of mangroves within each pixel (i.e., 25 km^2) (Giri et al. 2011) based on the OR Boolean operator.

1.2 Projection of rasters

All rasters were transformed into the Eckert-IV equal-area pseudocylindrical map projection. The agro-climatically attainable yields for oil palm and sugarcane, the cost distance to current oil palm and sugarcane cultivation areas, and the potential annual gross economic rents from agricultural lands, were resampled to a resolution of 5 × 5 km by using the Nearest Neighbor resampling method. The number of vertebrate species, the number of threatened vertebrate species, and the number of species with small distribution ranges, were resampled to a resolution of 5 × 5 km based on the Bilinear Interpolation resampling method.

Table S1. Description of layers and membership functions used for the development of a profitability model for biofuel production from microalgae, oil palm, and sugarcane; and for the construction of layers on agricultural and biodiversity value. Sigmoid Large: Larger input values result in higher suitability. Sigmoid Small: Lower input values result in higher suitability. Not Applicable (NA).

Layers	Description	Original spatial resolution for rasters	Type of function	Midpoint	Source
Proximity to rivers	Cost distance to permanent rivers with annual discharge ≥1.8 km^3 year^{-1}. Based on annual peak discharge.	NA	Sigmoid Small	50 km	Layer based on HydroSHEDS (Lehner et al. 2008), Vmap0 for permanent streams http://gis-lab.info/qa/vmap0-eng.html and river bankfull width (Andreadis et al. 2013).
Proximity to irrigation dams	Cost distance to irrigation dams with annual recharge ≥ 1.8 km^3 year^{-1}	NA	Sigmoid Small	50 km	GRanDv1 database (Lehner et al. 2011).
Proximity to fresh/brackish/ salt groundwater sources	Cost distance to fresh/brackish/salt groundwater global aquifers with annual recharge ≥ 1.8 km^3 year^{-1}. Excludes areas with complex hydrogeological structures, and areas with local and shallow aquifers.	NA	Sigmoid Small	50 km	Groundwater Resources of the World 1: 25 000 000. (BGR & UNESCO 2008).
Water depletion	Water availability based on the fraction of renewable water consumptively used for human activities within a watershed.	NA	NA. See Table S2	NA	Layer based water depletion metric within watersheds (Brauman et al. 2016).
Aridity index	Quantification of precipitation availability over atmospheric water demand by 2050. Aridity Index (AI) = MAP/MAE, where MAP = Mean Annual Precipitation and MAE = Mean Annual potential Evapotranspiration. Future mean annual precipitation and mean annual potential evapotranspiration were calculated based on an ensemble model for the Representative Concentration Pathway (RCP) 8.5 (i.e., high-emissions climate change scenario), by using the following General Circulation Models (GCMs): BCC-CSM1-1, CCSM4, GISS-E2-R, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM-CHEM, MRI-CGCM3, and NorESM1-M (Hijmans et al. 2005) (Chapter 3).	30 arcseconds	Sigmoid Large	1 for microalgae and oil palm (Adzemi 2014), 1.3 for sugarcane (FAO 2018)	Global aridity and PET database (Trabucco and Zomer 2009).
Proximity to oceans	Cost distance to oceans.	NA	Sigmoid Small	50 km	Oceans v.3.00 http://www.naturalearthdata.com
Microalgal lipid productivity	Prediction of lipid productivity based on 4,388 lipid point estimates for the cultivation of *Nannochloropsis* sp. in photobioreactors (Moody et al. 2014) by 2050, using as predictors annual mean radiation and the residuals of mean annual temperature explained by radiation. Future mean annual temperature was obtained based on an ensemble model for the Representative Concentration Pathway (RCP) 8.5 (i.e., high-emissions climate change scenario), by averaging mean annual temperatures among the following General Circulation Models (GCMs): BCC-CSM1-1, CCSM4, GISS-E2-R, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM-CHEM, MRI-CGCM3, and NorESM1-M (Hijmans et al. 2005). (Chapter 3).	5 × 5 km	Linear	NA	Layer based on lipid productivity estimates (Moody et al. 2014), and WorldClim v.1.4 and v2 (Hijmans et al. 2005).
Agro-climatically attainable yield	Attainable yield for oil palm and sugarcane by 2050, based on radiation, temperature, water balances, and optimal crop calendars. Irrigation and high-input management practices (i.e., high-yielding varieties and high crop densities) were considered.	300 arcseconds	Linear	NA	Global Agro-Ecological Zones GAEZ (IIASA/FAO 2012).
Availability of flat lands	Terrain slope.	30 arcseconds	Sigmoid Small	5°	Layer derived from GTOPO30 DEM https://lta.cr.usgs.gov/GTOPO30
Proximity to transport networks	Cost distance to roads and railroads.	NA	Sigmoid Small	50 km	Roads and railroads v. 3.0.0 http://www.naturalearthdata.com
Proximity to current cultivation areas	Cost distance to current oil palm and sugarcane cultivation areas.	10 × 10	Sigmoid Small	300 km	Layer based on current cultivation areas for oil palm and sugarcane, considering the Spatial Production Allocation

					Model SPAM 2005 v2.0. (≥ 100 ha pixel^{-1}) (You et al. 2014) and oil palm cultivation polygons (Furumo and Aide 2017).
Agricultural value	Potential annual gross economic rents from agricultural lands.	300 arcseconds	Linear	NA	Potential annual gross economic rents from agricultural lands (Naidoo and Iwamura 2007).
Number of vertebrate species	Number of vertebrate species (amphibians, birds, and mammals) based on IUCN species distribution maps, Bird Life International, and Nature Serve.	10 × 10 km	Linear	NA	Biodiversity maps (Jenkins et al. 2013).
Number of threatened vertebrate species	Number of vertebrate species (amphibians, birds, and mammals) based on IUCN distribution maps, Bird Life International, and Nature Serve.	10 × 10 km	Linear	NA	Biodiversity maps (Jenkins et al. 2013).
Number of vertebrate species with small distribution ranges	Number of vertebrate species with small distribution ranges (amphibians, birds, and mammals) based on IUCN distribution maps, Bird Life International, and Nature Serve.	10 × 10 km	Linear	NA	Biodiversity maps (Jenkins et al. 2013).
Presence of areas with low human pressures	Measure of human pressures (no pressure, low pressure, moderate pressure, high pressure, very high pressure) based on the presence of built environments, croplands, pastures, human population density, night-time lights, railways, roads, and navigable waterways.	1 × 1 km	Sigmoid Small	4	Human footprint (Venter et al. 2016)
Presence of islands	Islands	NA	Sigmoid Small	5000 km^2	Layer based on GADM database http://gadm.org/
Presence of mangroves	Percentage of mangroves covering each pixel (i.e., 25 km^2).	NA	Linear	NA	Global distribution of mangroves (Giri et al. 2011).

Table S2. Reclassification of original values for water depletion categories (Brauman et al. 2016) into suitability values ranging from 0 to 1.

Water depletion categories	Reclassified values
<5% depleted	0.95
5–25% depleted	0.75
25–50% depleted	0.5
50–75% depleted	0.25
Dry-year depleted	0.25
Seasonally depleted	0.25
75–100% depleted	0
100% depleted	0

2. Calculation of productivity values per pixel

For microalgal and oil palm cultivation, potential productivities per pixel (GJ pixel^{-1} year^{-1}) were calculated based on the following formula:

$$D = L_p * 0.81 * 0.0326$$

Where D corresponds to productivity values in units of energy (GJ pixel^{-1} year^{-1}), L_p corresponds to lipid production (L pixel^{-1} year^{-1}), 0.81 is the assumed proportion of biodiesel produced from an initial volume of lipids contained in microalgal cells or oil palm fruits (assuming a lipid extraction efficiency of 0.9 and a conversion efficiency from lipids to biodiesel of 0.9), and 0.0326 (GJ L^{-1}) corresponds to the Low Heating Value conversion factor from a volume of biodiesel to energy (Hofstrand 2008).

For microalgae, lipid production was calculated based on Moody et al. (2014) (see section 1 in Supplementary Information). For oil palm, lipid production was calculated based on the following formula:

$$L_p = \frac{Y}{0.225} * \frac{0.26}{9.2 * 10^{-4}} * 2500$$

Where L_p corresponds to lipid production (L pixel^{-1} year^{-1}), Y corresponds to the agro-climatically attainable yield (t ha^{-1} year^{-1} in dry weight), 0.225 is the conversion factor from fresh weight to dry weight for oil palm fruits (IIASA/FAO 2012), 0.26 is the proportion of lipids in oil palm fruits (El

Bassam 2010), $9.2 * 10^{-4}$ is the palm oil density (t L^{-1}) (Firestone 2013), and 2500 corresponds to the number of hectares per pixel (ha $pixel^{-1}$).

For sugarcane cultivation, potential productivities per pixel (GJ $pixel^{-1}$ $year^{-1}$) were calculated based on the following formula:

$$D = \frac{Y}{0.1} * 83 * 2500 * 0.0211$$

Where D corresponds to productivity values in units of energy (GJ $pixel^{-1}$ $year^{-1}$), Y is the agro-climatically attainable yield (t ha^{-1} $year^{-}$1 in dry weight), 0.1 is the conversion factor from fresh weight to dry weight for sugarcane (IIASA/FAO 2012), 83 is the conversion efficiency from an initial fresh weight of sugarcane into bioethanol (L t^{-1}) (de Vries et al. 2010), 2500 corresponds to the number of hectares per pixel (ha $pixel^{-1}$), and 0.0211 corresponds to the Low Heating Value conversion factor from a volume of bioethanol to energy (GJ L^{-1}) (Hofstrand 2008).

Chapter 5. Contribution to the authorship

I was in charge of the conception and design of the project; acquisition, analysis, and interpretation of the research data; drafting, analysis, and critical writing of the manuscript; and sending of the manuscript to peer-reviewed journals (i.e., as corresponding author).

CHAPTER 5. Towards the implementation of sustainable biofuel production systems

Diego F. Correa[1, 2*], Hawthorne L. Beyer[2], Joseph E. Fargione[3], Jason D. Hill[4], Hugh P. Possingham[2,5], Skye R. Thomas-Hall[1], Peer M. Schenk[1]

[1]Algae Biotechnology Laboratory, School of Agriculture and Food Sciences, The University of Queensland, Brisbane, QLD 4072, Australia

[2] Centre for Biodiversity and Conservation Science CBCS, The University of Queensland, Brisbane, Queensland 4072, Australia

[3] The Nature Conservancy, Minneapolis, MN 55415, USA

[4] Department of Bioproducts and Biosystems Engineering, The University of Minnesota, St. Paul, MN 55108, USA

[5] The Nature Conservancy, Arlington, VA 22203, USA

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HIGHLIGHTS

- First generation biofuels are the least sustainable biofuel production alternative
- Implementing more sustainable biofuel production systems is urgently needed
- Sustainable biofuels need the integration of socioeconomic and environmental goals
- Economic barriers to adopt these systems can be overcome through policy mechanisms

ABSTRACT

Novel energy production systems are needed that not only offer reductions in greenhouse gas emissions but also cause fewer overall environmental impacts. How to identify and implement more sustainable biofuel production alternatives, and how to overcome economic challenges for their implementation, is a matter of debate. In this study, the environmental impacts of alternative approaches to biofuel production (i.e., first, second, and third generation biofuels), with a focus on biodiversity and ecosystem services, were contrasted to develop a set of criteria for guiding the identification of sustainable biofuel production alternatives (i.e., those that maximize socioeconomic and environmental benefits), as well as strategies for decreasing the economic barriers that prevent the implementation of more sustainable biofuel production systems. The identification and implementation of sustainable biofuel production alternatives should be based on rigorous assessments that integrate socioeconomic and environmental objectives at local, regional, and global scales. Further development of environmental indicators, standardized environmental assessments, multi-objective case studies, and globally integrated assessments, along with improved estimations of biofuel production at fine spatial scales, can enhance the identification of more sustainable biofuel production systems. In the short term, several governmental mandates and incentives, along with the development of financial and market-based mechanisms and applied research partnerships, can accelerate the implementation of more sustainable biofuel production alternatives. The set of criteria and strategies developed here can guide decision making towards the identification and adoption of sustainable biofuel production systems.

Keywords: Biodiversity, biofuel, bioenergy, climate change, microalgae, renewable energy, ecosystem service

1. INTRODUCTION

Boosting economic growth while halting environmental degradation remains one of the major global challenges for humankind (Raudsepp-Hearne et al. 2010). Current unsustainable use of the Earth’s finite natural capital (Hoekstra and Wiedmann 2014) has led to a wide range of negative impacts on the environment (Rockström et al. 2009), including increasing biodiversity losses (Ceballos et al. 2015), alterations in the provision and quality of ecosystem services (Lawler et al. 2014), and climate change (Cox et al. 2000). These impacts and the decisions that society makes to reduce them, which include balancing human population growth (Crist et al. 2017) and planning for solutions based on multiple interacting environmental pressures (Watson 2014), will have profound implications for global socioeconomic and environmental systems.

How to meet increasing energy consumption demands, while reversing environmental degradation, is a matter of debate (Heard et al. 2017). Currently, the provision of energy relies primarily on fossil fuels, with around 5.8×10^{11} GJ consumed globally in 2016, of which 81% was derived from coal, petroleum, and natural gas (IEA 2017). Their associated greenhouse gas (GHG) emissions are linked to global warming and its negative impacts on biodiversity (Pecl et al. 2017) and ecosystem services (Scholes 2016). Limiting global warming to well below 2°C compared to pre-industrial levels, a goal ratified or acceded by 185 parties (i.e., on February 2019) following the 21st Conference of the Parties to the United Nations Framework Convention on Climate Change (UNFCCC) in Paris (IPCC 2015), is expected to require the rapid adoption of renewable energy systems for replacing fossil fuels (Walsh et al. 2017). Consequently, the share of energy from renewable sources could increase from 9% of total primary energy demands in 2016 to 29% by 2040 (IEA 2017).

While solar, wind and water as renewable energy sources could provide electricity with lower environmental costs compared to fossil fuels (Jacobson and Delucchi 2011), liquid fuels are expected to remain necessary in the transport sector—mainly for aviation, shipping, and long-haul trucking—in spite of an expected increase in electric vehicles (Fulton et al. 2015). In fact, some scenarios for limiting global warming to 2°C, foresee biofuel production increasing from 9.7×10^{6} GJ d^{-1} to 4.6×10^{7} GJ d^{-1} between 2016 and 2040, reaching 16% of total transport fuels (IEA 2017), though it remains unclear to what degree biofuel adoption would reduce net GHG emissions compared to other climate change mitigation options (Righelato and Spracklen 2007).

Current biofuel production is based on food crops (i.e., first generation biofuels) that compete with agricultural lands and biodiverse landscapes (Box 1, Fig. 1). Furthermore, biofuel production has been linked to several other environmental pressures that may, directly and indirectly, impact biodiversity and the provision of ecosystem services. These pressures (Correa et al. 2017) include direct and indirect land-use change (Immerzeel et al. 2014), GHG emissions (Fargione et al. 2008), emission of pollutants (i.e., from pesticides, fertilizers, biofuel production, and final use of biofuels) (Hill et al. 2006), water depletion (Gerbens-Leenes et al. 2009), soil degradation and erosion (Gregg and Izaurralde 2010), and introduction of invasive species (Barney and DiTomaso 2008). The impacts of biofuels on biodiversity and ecosystem services, however, depend on the type of biofuel production system and several factors associated with its cultivation and production (Immerzeel et al. 2014), including: the competing land-use and the spatial configurations of biofuel cultivation landscapes (Koh et al. 2009), their cultivation and conversion technologies (Hill et al. 2006), their cultivation management practices (Fargione et al. 2009), their invasiveness potential (Barney and DiTomaso 2011), and the presence of co-products (Box 2) (Fargione et al. 2010).

Box 1. Biofuels, main production regions, and overlapping areas of high ecological importance

Biofuel production involves the transformation of organic compounds—including cellulose, hemicellulose, lignin, starch, saccharose, and oils—from living organisms into carbon-rich carriers (e.g., alcohols and esters) that can be used for energy generation (Kamm and Kamm 2004). These organic compounds can come from a wide range of feedstocks (i.e., the range of sources from which biofuels are produced), including herbaceous and woody plants, oilseeds, agricultural and forestry wastes, and algae (Naik et al. 2010). Feedstocks are transformed into biofuels through various combinations of thermochemical, biochemical, chemical and physical processes depending on feedstock properties (e.g., moisture content, proportions of fixed carbon and volatile matter, and cellulose/lignin ratios) (McKendry 2002). Different environmental impacts, including habitat loss for native species (Immerzeel et al. 2014), GHG emissions (Fargione et al. 2008), emission of pollutants (Hill et al. 2006), and water withdrawals (Gerbens-Leenes 2018), arise from combinations of feedstock cultivation systems and their processing technologies.

According to REN21 (2016), 133 × 10^9 L of liquid biofuels were produced in 2015, mainly in the forms of bioethanol (98.3 × 10^9 L, contributing to 74% of global biofuel production) and biodiesel (30.1 × 10^9 L, contributing to 23% of global biofuel production). Bioethanol production was led by the USA (57% of the total global bioethanol production), followed by Brazil (29%) and the EU-28 (4%), mostly from maize in the USA, maize and wheat in the EU-28, and sugarcane in Brazil. Biodiesel production was led by the EU-28 (38% of the global total production), followed by the USA (16%) and Brazil (14%) (REN21 2016), primarily from rapeseed in Europe, and soybean in the USA and Brazil. Another widely used biodiesel feedstock is oil palm (Mekhilef et al. 2011). Cultivation of these crops overlaps with areas of high ecological importance, and have widely replaced native ecosystems, including native grasslands in the USA (Morefield et al. 2016) and Brazil (WWF 2016), as well as tropical and subtropical forests in South America (Barona et al. 2010) and Southeast Asia (Vijay et al. 2016).

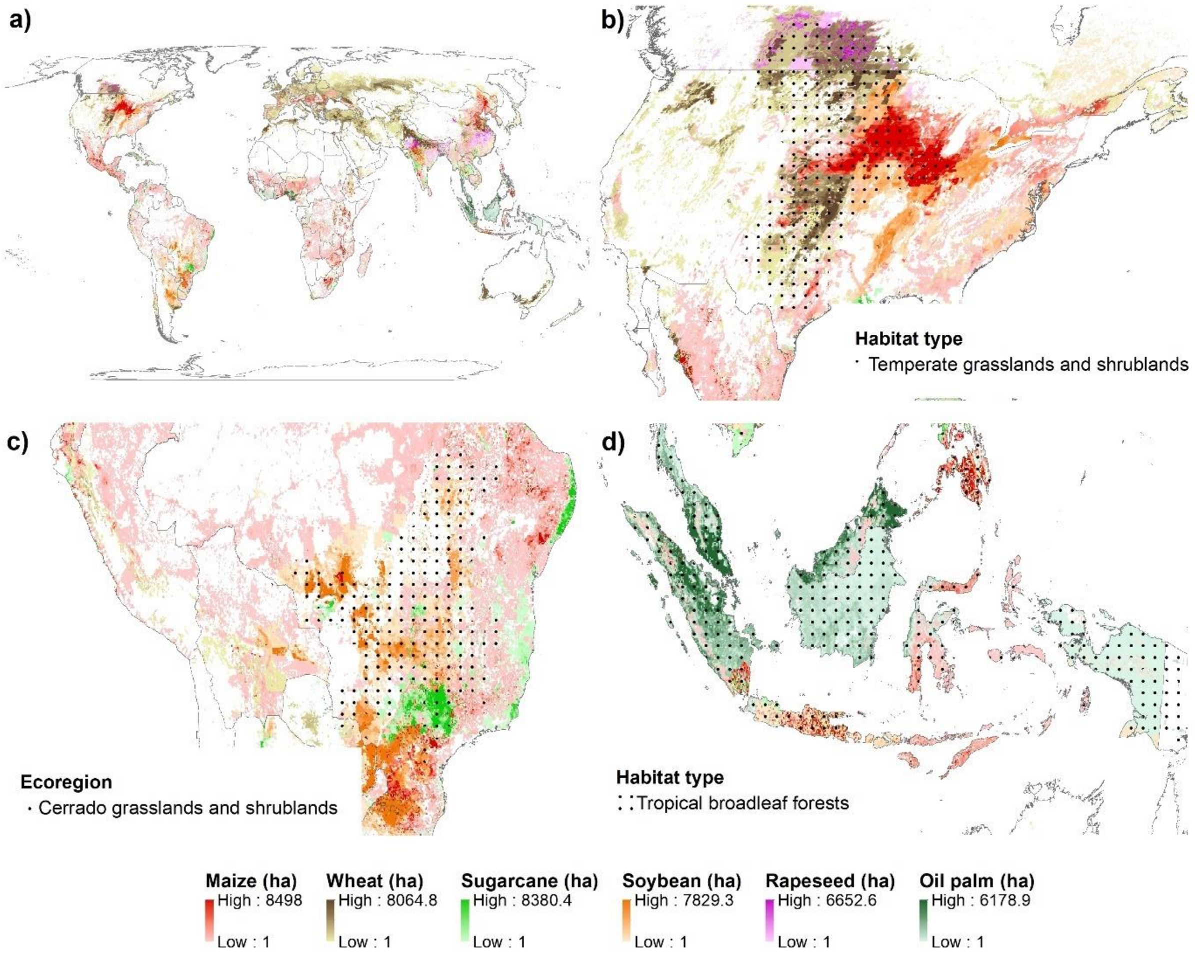

Figure 1. Cultivation areas of food crops used for biofuel production globally (a) and overlapping habitat types and ecoregions (as dotted areas) (TNC 2009) in North America (b), South America (c) and South East Asia (d). Total physical cultivation area for crops is based on the Spatial Production Allocation Model (SPAM) 2005 v.2.0 at 5 arcmin grid cells (You et al. 2014).

Box 2. Factors that modify the environmental impacts of biofuel production

The impacts of biofuel production on biodiversity and ecosystem services are modified by:

- Competing land-use: Determines how much GHG will be emitted (Searchinger 2010) and how much biodiversity will be lost (Immerzeel et al. 2014) after the replacement of original systems by biofuel production systems. The transformation of native ecosystems leads to fragmentation, habitat losses, and large CO_2 emissions arising from losses in biomass and soil carbon contents (Fargione et al. 2010). The competition with agricultural lands increases the potential for indirect land-use changes (Lambin and Meyfroidt 2011), leading to increases in CO_2 emissions, further biodiversity losses and environmental degradation outside biofuel cultivation areas (Fargione et al. 2010).
- Spatial configurations of cultivation landscapes: Modifies the likelihood of species persistence at local and landscapes scales, as well as the provision of ecosystems services. For instance, a combination of intensive production areas, agroforestry systems, and forest patches (i.e., land-sparing) has been proposed as a way to maintain regional biodiversity and ecosystem services for oil palm cultivation

(Koh et al. 2009). Alternatively, biofuel cultivation areas could be managed to promote higher biodiversity (i.e., land-sharing) (Manning et al. 2015). Jager and Kreig (2018) propose the conservation of large patches of native ecosystems, the implementation of biological corridors at landscape scales (i.e., land-sparing), and the reduction of production intensity at the scale of parcels (i.e., land-sharing).

- Biofuel cultivation and conversion technologies: Determines how much GHGs will be saved in comparison to fossil fuels, as a balance between inputs (e.g., fertilizers, energy used for converting feedstocks into biofuels) and products (i.e., biofuels and co-products) (Hill et al. 2006). Affects water withdrawal (Gerbens-Leenes et al. 2014) and the amount of emitted pollutants during the cultivation and processing of feedstocks (Hill et al. 2006), as well as the overall environmental impacts associated with biofuel production (Correa et al. 2017).
- Cultivation management practices: Modifies the magnitude of ongoing GHG emissions depending on how much fertilizer is used (Hill et al. 2006) and how soil is disturbed (e.g., frequent vs. sporadic soil tillage) (Paustian et al. 2000). For instance, Qin et al. (2018) found that reducing tillage in USA maize-soybean production systems can offset GHG emissions derived from corn stover harvesting. Affects soil erosion rates, as well as pollution potential within and outside cultivation areas as a result of pesticide and fossil fuel use (Correa et al. 2017). Impacts the persistence of native species within production areas (Fargione et al. 2009).
- Invasiveness potential: Affects the local and regional persistence of native species, as well as the resilience of natural systems and their associated ecosystems services (Barney and DiTomaso 2008).
- Co-products: Affects the sustainability of biofuel production systems, as well as the emission of GHGs, pollutants, and energy efficiencies (Hill et al. 2006). Can help in offset GHG emissions (Creutzig et al. 2015) and reduce external energy inputs dependent on fossil fuels (Slade and Bauen 2013).

How to identify and implement more sustainable biofuel production alternatives (Darda et al. 2019), and how to overcome economic obstacles to their implementation, are unresolved challenges (Soares et al. 2018). Here, the environmental impacts of several biofuel production alternatives (i.e., first, second, and third generation biofuels) on biodiversity and ecosystem services are evaluated. This information is integrated with criteria and avenues of research for guiding the identification and implementation of sustainable biofuel production alternatives (i.e., those that maximize socioeconomic and environmental benefits). Finally, promising strategies for overcoming economic barriers to adopt more sustainable biofuel production systems, are discussed.

2. An overview of the environmental impacts of several biofuel production alternatives

First generation biofuels, which compete with agricultural and biodiverse lands, have led to habitat loss for native species (Elshout et al. 2019) and associated GHG emissions (Fargione et al. 2008) (Box 3). This mainly occurs by the direct replacement of biodiverse and carbon-rich original systems (i.e., direct land-use change) (Immerzeel et al. 2014), and by the agricultural expansion outside biofuel production areas (Lambin and Meyfroidt 2011) as a consequence of increases in food prices generated by the competition with food production (i.e., indirect land-use change) (To and Grafton 2015). For instance, between 1990 and 2005 in Southeast Asia, more than 55% of oil palm crops—which is used for human consumption and as a source for biodiesel production—came from oil palm plantations on converted native forests, directly increasing the extinction risk of thousands of species (Fitzherbert et al. 2008), while emitting large amounts of CO_2 into the atmosphere (Fargione et al. 2008). In Borneo, Sumatra and Peninsular Malaysia alone, it is estimated that the conversion of 6% of peat-swamp forests into oil palm by the early 2000s, led to direct emissions of more than 140 Mt of CO_2 into the atmosphere plus ongoing annual carbon losses of around 4.6 Mt as a result of peat oxidation (Koh et al. 2011). Conversion of peat-swamps and associated releases of CO_2 are ongoing (Miettinen et al. 2016). The expansion of first generation biofuels has also impacted South America, where soybean cultivation—used for food, animal feed, and biodiesel production—has directly replaced large areas of the biodiverse Cerrado savannas (WWF 2016), and indirectly driven deforestation in the Amazon forest for cattle production (Barona et al. 2010). In North America, bioethanol production from maize has, directly and indirectly, promoted the replacement of native and planted grasslands (Lark et al. 2015). Further cultivation of food crops for biofuel production threatens many other biodiverse and carbon-rich systems, including the African savannas (Searchinger et al. 2015) and several other suitable agricultural areas mainly in the highly productive tropical regions (Laurance 2015), as well as in developing economies with high energy demands (e.g., China) (Qin et al. 2018).

GHGs—including CO_2, methane (CH_4), nitrous oxide (N_2O), and carbon monoxide (CO)—as well as air pollutants—including ammonia (NH_3), volatile organic compounds (VOC), particulate matter (PM), nitrogen oxides (NO_x), and sulfur oxides (SO_x) (Zhang et al. 2016)—are emitted during the replacement of original systems (Searchinger et al. 2008), cultivation and processing of feedstocks (Snyder et al. 2009), transportation of biofuels to fuel stations, and final use of biofuels (Creutzig et al. 2015). For instance, the emission of N_2O during the cultivation of crops with high nitrogen demands can offset CO_2 savings, as its global warming potential is 296 times larger than an equal mass of CO_2 (Crutzen et al. 2008). Air pollution not only contributes to climate change, but also, directly and indirectly, impact species, ecosystems , and humans (e.g., through poisoning, acid rain, ozone layer depletion, tropospheric ozone formation, and changes in regional weather patterns) (Heijungs et al. 1992). In fact, Tessum et al. (2014) show that replacing conventional gasoline with corn ethanol in USA light-duty transportation can increase environmental health impacts by 80% from increased levels of O_3 and PM.

Box 3. The controversial GHG emissions of biofuels

In biofuel production systems, GHGs are emitted as a result of land-use changes (Fargione et al. 2008), as well as during the cultivation of feedstocks (Snyder et al. 2009), their harvesting, and their processing into biofuels (i.e., CO_2 emissions through soil disturbance, heterotrophic respiration, biomass combustion, and the use of energy-intensive processes) (DeCicco 2013). Further CO_2 emissions occur as a result of the production and transportation of inputs required for biofuel production (e.g., fertilizers), the transport of biofuels to fuel stations, and the final burning of biofuels for energy production (Hill et al. 2006). Other GHGs, including CH_4, N_2O, and CO are additionally emitted during the production and use of biofuels (Zhang et al. 2016). Currently, the accounting of GHGs derived from biofuel production as well as the definitive role of biofuel in climate change mitigation, remain controversial (Creutzig et al. 2015). However, in relation to CO_2 emissions, some consensus exists:

- To offset the CO_2 emitted by biofuel production, the carbon uptake during cultivation should be higher than the counterfactual reference system (Searchinger 2010). For instance, in Southeast Asia, it would take between 86 and 423 years to fix the CO_2 emitted when lowland rainforests and peatland rainforests are, respectively, transformed into oil palm plantations (Fargione et al. 2008). Even in systems with lower carbon stocks (e.g., grasslands), carbon emissions would be substantial. Searchinger et al. (2015) estimate that in 99.4% of Africa’s wet savannas more than 10 years would be needed to fix the CO_2 emitted following their replacement by second generation biofuels.
- CO_2 emissions can decrease through the use of carbon-efficient cultivation and conversion practices and technologies. This includes the use of systems with lower fertilizer use (e.g., soybean cultivation would need fewer fertilizers than maize) (Hill et al. 2006), the avoidance of detrimental soil management practices that drive carbon losses (e.g., reduced soil tillage) (Paustian et al. 2000), and the optimization of energy-intensive processes for feedstock harvesting and conversion into biofuels (e.g., use of anaerobic digestion for nutrient recycling and energy production in microalgal production systems) (González-González et al. 2018).
- Carbon can be additionally captured and sequestered in long-term geological scales, for instance, using systems of bioenergy with carbon capture and storage (BECCS) (Popp et al. 2017).

In the face of future agricultural expansion, alternatives that do not compete with food production or with biodiversity, and with fewer direct and indirect impacts on biodiversity and ecosystem services are needed to replace fossil fuels (Box 4, Fig. 2). Second generation biofuels, based on the transformation of the abundant lignin and cellulose found in non-food plants such as *Miscanthus* (Heaton et al. 2008) and *Jatropha* (Silitonga et al. 2011, van Eijck et al. 2014), as well as in organic wastes (Naik et al. 2010), could lower competition with prime agricultural lands used for food production, as well as decrease the use of water, fertilizers, and pesticides (Eisentraut 2010). The cultivation of second generation biofuels (e.g., willow, poplar, *Eucalyptus*, *Miscanthus,* and switchgrass) could, however, compete with important areas for biodiversity conservation (Beringer et al. 2011), become invasive (Barney and DiTomaso 2008), drive soil water depletion in dry areas (Yimam et al. 2014)—e.g., *Eucalyptus* plantations in Australia (Robinson et al. 2006) and *Miscanthus* plantations in the Midwest USA) (Vanloocke et al. 2010)—and emit considerable amounts of air pollutants including PM, NO_x, SO_x, NH_3, and VOCs (Thakrar et al. 2017). Further negative impacts on key ecosystem services (e.g., water availability, disease and pest control, pollination, soil and water quality) would be expected when replacing forests and grasslands with second generation biofuels (Holland et al. 2015). Additionally, indirect land-use changes would likely occur if demands for forest biomass increase, which would create incentives for further deforestation, particularly in tropical regions (Phalan 2009).

Box 4. Future agricultural expansion, biofuels, and biodiversity

Current species extinction rates are estimated at between 100 (Ceballos et al. 2015) and 1,000 times greater (Rockström et al. 2009) than those found in fossil records. For vertebrates, around 25% of mammal species, 13% of birds and 42% of amphibians are currently classified under some extinction threat category (IUCN 2016), and average losses in global population abundances are calculated at 58% between 1970 and 2012 (WWF 2016). Additionally, 20–50% of the original extent of nine of the 14 world's biomes has been transformed into croplands, with a notable loss of tropical dry forests, temperate grasslands, temperate broadleaf forests and Mediterranean forests (MEA 2005). As biodiversity continues to be negatively impacted by human activities—as a result of land-use change, fragmentation of native ecosystems, pollution, occurrence of invasive species, and climate change (MEA 2005)—not only will more species risk extinction, but also ecosystem resilience will decrease, affecting the provision of multiple ecosystem services and ultimately the human wellbeing (Costanza et al. 1997).

Increases in food and energy demands are expected to drive further pressures on biodiversity and ecosystem services, particularly when using biofuels derived from food crops (Correa et al. 2017). Currently, around 34%

of global terrestrial lands are used for agriculture, including 1.6 × 10^9 ha of rainfed and irrigated croplands, and 3.4 × 10^9 ha of pastures used for animal grazing (Alexandratos and Bruinsma 2012). At a population projection of around 9,000 million people by 2050, it is expected that food demands will increase by more than 60% from 2006 levels (FAO 2016), which could lead to an expansion of around 70 million ha for croplands, assuming that yields rise within current production systems (Alexandratos and Bruinsma 2012). This expansion is expected to occur mostly in tropical developing countries, placing additional pressures on tropical ecosystems (Laurance 2015).

Biofuel production systems that compete with agricultural lands are not only likely to threaten food production (Fischer et al. 2009), but also are expected to magnify the environmental pressures and impacts on biodiversity and ecosystem services (Liu et al. 2015).

Intercropping biofuels in agricultural areas or timber plantations would also help in reducing competition with food production (Tilman et al. 2009). However, they could disturb native species that make use of the plantations depending on management practices (Robertson et al. 2012) and, under some conditions, drive losses in soil carbon stocks. For instance, Strickland et al. (2015) found that intercropping switchgrass within *Pinus taeda* plantations can reduce soil carbon during the first years following switchgrass planting.

While using wastes for biofuel production does not directly compete with agricultural or biodiverse lands, they could impact biodiversity and ecosystem services. For instance, the extraction of agricultural and forestry wastes can decrease soil carbon stocks and fertility in cultivation areas (Anderson-Teixeira et al. 2009), negatively impact species that make use of decaying biomass (Riffell et al. 2011), and indirectly drive deforestation as demand for biomass increases (Phalan 2009). On the other hand, the use of plantations of native perennials on low-biodiversity or degraded lands could enhance the provision of several ecosystem services including carbon storage and pollination (Werling et al. 2014), as well as reduce the use of fertilizers and pesticides compared to conventional crops, allow the persistence of grassland or shrubland species, and reduce competition with food crops (Tilman et al. 2009).

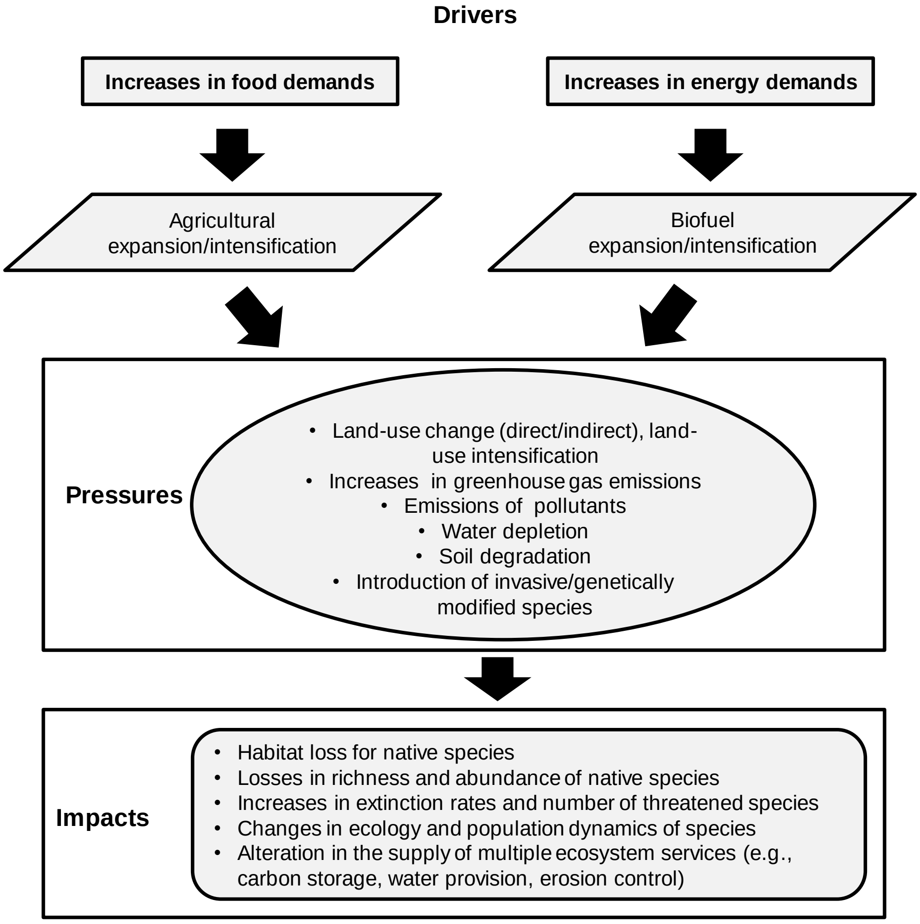

Figure 2. Magnification of pressures and impacts on biodiversity and ecosystem services exerted by the combined expansion of agriculture and first generation biofuels for meeting food and energy demands. Pressures are defined as anthropogenic factors that induce environmental impacts, based on the DPSIR framework (Kristensen 2004).

Third generation biofuels are mainly based on the use of microalgae (Box 5). This technology can be optimized to produce several types of biofuels, including biodiesel, bioethanol, biogas, and biohydrogen (Schenk et al. 2008). Because of high microalgal biomass productivities, microalgal systems require significantly less cultivation area to meet the same amount of energy compared to first and second generation biofuel crops (Table 1), particularly in areas with high solar radiation and high mean annual temperatures (Correa et al. 2017). They do not require fertile soils, and so are not expected to drive direct or indirect land-use changes within agricultural areas or biodiverse regions (Usher et al. 2014). Several strains can be cultivated in brackish water or seawater (Maeda et al. 2018), reducing competition with freshwater, and their dependence on environmental pollutants such as pesticides is lower compared to other terrestrial crops (Smith et al. 2010). Furthermore, microalgal production systems can make use of residual CO_2 from industries (because supplementing algae production systems with CO_2 increases algal growth) and nutrients from wastewater, helping in carbon capture (Sayre 2010) and water remediation (Mu et al. 2014).

Although several potential environmental impacts of large-scale microalgal production systems remain unclear (e.g., carbon balances, nutrient use, invasiveness potential, pollution of aquatic ecosystems) (Slade and Bauen 2013), the development of more efficient cultivation and processing technologies that make use of renewable energy sources can improve the net GHG balances of microalgal production systems (Collet et al. 2014). Furthermore, the recycling of culture media (Yang et al. 2011) and biomass residues (e.g., after lipids are extracted for biodiesel production), can reduce the use of freshwater (Gerbens-Leenes et al. 2014) and fertilizers (González-González et al. 2018), while decreasing the risk of polluting aquatics ecosystems (Usher et al. 2014), and the cultivation of microalgae with low invasiveness potential can avoid unintended ecological changes in surrounding aquatic environments (Committee on the Sustainable Development of Algal Biofuels et al. 2012).

Box 5. Microalgal biofuel production: Higher productivities per unit area than other biofuel production crops

Prokaryotic (i.e., cyanobacteria) and eukaryotic microalgae (e.g., green algae, red algae, and diatoms) can be cultivated for producing biogas, bioethanol, biodiesel, and biohydrogen (Mata et al. 2010). Other products, including biochar, high-value compounds for human consumption, as well as fertilizer or animal feed can also be produced from microalgae (Brennan and Owende 2010).

Algae growth requires CO_2, light, and a growing medium with inorganic salts (i.e., water with nutrients such as nitrogen, phosphorus, iron, and silicon) (Chisti 2007). Maximum productivities are achieved at high light intensities and constant high temperatures (usually between 20 and 30°C) (Chisti 2007), and at a pH optimal to each microalgal strain (Schenk et al. 2008). Biomass productivities increase when supplemented with CO_2 (Nascimento et al. 2015), and when growth conditions are optimized to control algal grazers (Narala et al. 2016) and enhance biomass and lipid productivities (Ravindran et al. 2017).

Microalgae are among the most productive photosynthetic organisms on Earth (Chisti 2007). Estimates on lipid productivities range from 2,100 L ha^{-1} y^{-1} when cultivating *Spirogyra* sp. in urban wastewater ponds in India (Ramachandra et al. 2013) to 136,900 L ha^{-1} y^{-1} if growing species with high oil content in photobioreactors (Chisti 2007). According to Lundquist et al. (2010) in theoretical optimal conditions biomass yields could reach 290 t ha^{-1} y^{-1} within the continental USA (i.e., oil yields equal to 126,000 L ha^{-1} y^{-1}), assuming conversion efficiencies of 10% from solar energy into biomass, high annual irradiances (i.e., at 7,500 MJ m^{-2} y^{-1} in Yuma, Arizona) and cell lipid contents at around 40%. More conservative maximum oil yields are estimated at between 24,000 and 27,000 L ha^{-1} y^{-1}, which could be achieved within tropical countries with high solar irradiance (Moody et al. 2014). For instance, when cultivating *Scenedesmus dimorphus* under subtropical conditions (Brisbane, Australia) it is possible to produce 72 t ha^{-1} y^{-1} of dry biomass, equivalent to around 19,400 L ha^{-1} y^{-1} (based on cell lipid contents at around 25% and oil densities at 930 kg m^{-3}) (Schenk 2016).

This means that the land footprint of microalgal production systems would be substantially lower compared to any other biofuel production system, including first generation biofuels (Correa et al. 2017).

1. Identifying and implementing sustainable biofuel production alternatives

If humankind is to halt further biodiversity losses and overall environmental degradation while limiting global warming (IPCC 2015), the identification and implementation of biofuel production systems must ensure that overall socioeconomic and environmental benefits are achieved (Fig. 3). Price competitiveness, affordability (Demirbas 2009), and reliability in comparison to fossil fuels (Zah and Ruddy 2009) are essential for the deployment of biofuel production systems. Systems that are able to meet biofuel production targets (i.e., based on their high production levels or the availability of feedstocks), as well as those able to meet socioeconomic targets (Hunsberger et al. 2017) (e.g., welfare improvement in biofuel producing countries and local communities) (Singh 2013) (Box 6), could be preferred over others. Furthermore, biofuel production systems with lower environmental impacts (Demirbas 2009), or even environmental benefits, could contribute to achieve targets in carbon emission reductions, biodiversity conservation, and provision of ecosystem services (Tilman et al. 2009). These systems would need to provide large net GHG savings (including the avoidance of depleting existing carbon stocks in biomass and soil) (Tilman et al. 2006), avoid competition with agricultural lands (Tilman et al. 2009), avoid direct or indirect land-use changes in biodiverse areas (Correa et al. 2017), have low water footprints (Gerbens-Leenes et al. 2012), and minimize pollution (Hill et al. 2006), soil degradation (McLaughlin and Walsh 1998), and invasiveness potential (Raghu et al. 2011). Systems that maintain biodiversity and ecosystem services in the broader landscape (i.e., within and outside plantations) (Koh et al. 2009) could reduce regional biodiversity losses (Wiens et al. 2011) while maintaining ecosystems services (Werling et al. 2014).

Table 1. Cultivation area (thousand km^2) for fulfilling total transport energy demands for biggest energy consuming countries in 2016 (i.e., countries that account for 80% of world's total transport energy consumption), based on first (1G), second (2G), and third generation (3G) biofuels. The percentage of cultivation area (%) in relation to each country's land area is included. See Supplementary Information for details on calculations and Correa et al. (2017) for comparisons with other countries.

Country	1G biofuels												2G biofuels						3G biofuels	
	Ethanol						Biodiesel						Ethanol				Biodiesel		Biodiesel	
	Wheat		Maize		Sugarcane		Soybean		Rapeseed		Oil palm		Switchgrass		*Miscanthus*		*Jatropha*		Microalgae	
	Area	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**	**Area**	**%**
United States	10,094	106	2,987	31	1,922	20	14,119	149	11,014	116	-	-	3,524	37	1,153	12	4,681	49	622	7
China	2,905	31	2,422	26	1,009	11	11,515	122	4,997	53	1,242	13	1,679	18	549	6	2,229	24	353	4
Russia	2,003	12	989	6	-	-	5,000	30	2,574	15	-	-	531	3	174	1	-	-	157	1
India	1,483	47	1,624	51	306	10	5,707	180	2,412	76	-	-	-	-	-	-	673	21	66	2
Brazil	1,629	19	800	9	265	3	1,934	23	2,096	25	390	5	-	-	-	-	620	7	61	1
Japan	938	251	1,308	350	308	82	3,019	809	1,609	431	-	-	408	109	133	36	-	-	83	22
Canada	948	10	294	3	-	-	1,455	15	934	9	-	-	344	3	113	1	-	-	108	1
Germany	372	104	277	78	-	-	1,811	508	496	139	-	-	322	90	105	30	-	-	89	25
Mexico	503	26	751	38	174	9	2,370	121	1,573	80	222	11	-	-	-	-	396	20	39	2
Indonesia	-	-	457	24	200	11	2,228	117	-	-	155	8	-	-	-	-	353	19	36	2
Saudi Arabia	374	20	377	20	-	-	-	-	-	-	-	-	-	-	-	-	342	18	33	2
Iran	1,256	77	309	19	135	8	1,388	85	798	49	-	-	252	16	83	5	335	21	34	2
France	319	58	235	43	-	-	1,102	201	416	76	-	-	248	45	81	15	-	-	52	10
United Kingdom	261	107	-	-	-	-	-	-	374	153	-	-	231	95	76	31	-	-	68	28
Italy	462	154	182	60	-	-	728	242	479	159	-	-	203	68	67	22	-	-	35	12
South Korea	546	544	343	341	-	-	1,457	1450	1,118	1113	-	-	199	199	65	65	-	-	43	43
Australia	824	11	232	3	97	1	1,096	14	805	10	-	-	185	2	61	1	246	3	22	0
Spain	510	101	131	26	181	36	763	151	471	93	-	-	174	34	57	11	-	-	27	5
Turkey	498	64	150	19	-	-	451	58	246	32	-	-	150	19	49	6	-	-	25	3
Thailand	1,246	241	280	54	83	16	1,104	213	-	-	76	15	-	-	-	-	188	36	21	4
Malaysia	-	-	149	45	163	49	-	-	-	-	64	19	-	-	-	-	161	49	17	5
South Africa	281	23	192	16	69	6	766	63	443	36	-	-	-	-	-	-	141	11	14	1
Egypt	146	15	117	12	39	4	399	40	-	-	-	-	105	11	34	3	140	14	13	1

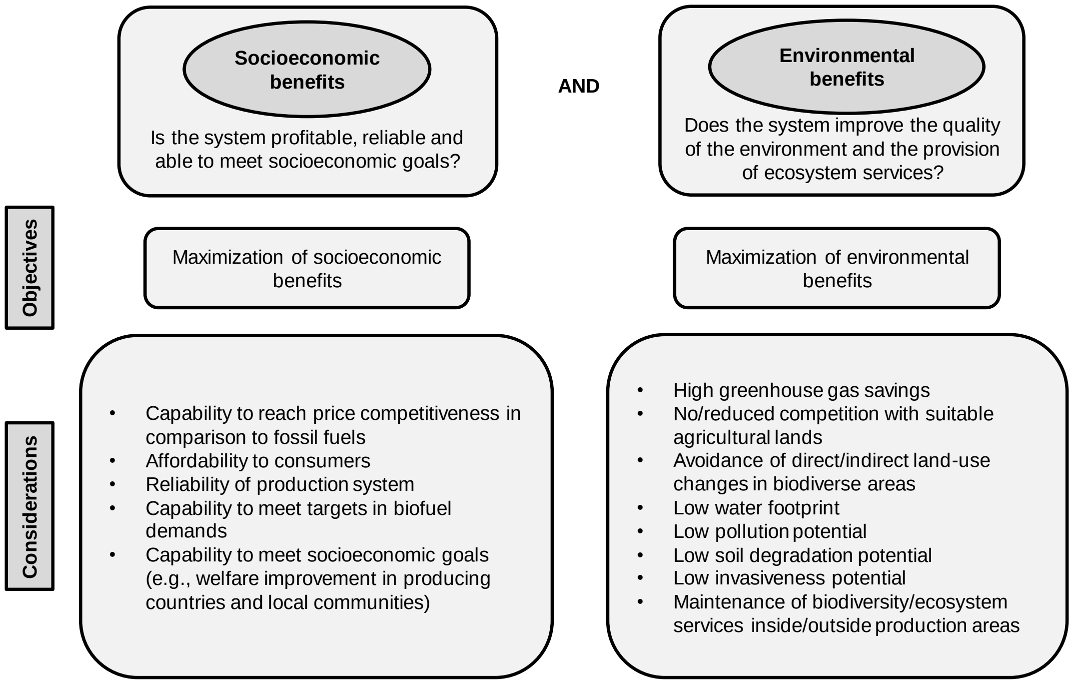

Figure 3. Criteria to be considered when evaluating the socioeconomic and environmental benefits of biofuel production systems.

Box 6. The social impacts of first generation biofuels

Biofuel production has been linked to a wide range of negative socioeconomic impacts, closely related to those exerted by large-scale farming systems. Controversies exist on the actual benefits of agricultural and biofuel expansion in developing countries, where rural poverty and informal land tenure are prevalent (Lawry et al. 2017). While the production of biofuels can bring economic incentives to developing nations and help in poverty alleviation through the creation of jobs (Ewing and Msangi 2009), it can negatively impact land rights (Phalan 2009), drive rises in land prices, as well as alienate, marginalize, and displace locals (Obidzinski et al. 2012). Biofuels have additionally been related to increases in food prices (To and Grafton 2015), directly affecting smallholder farmers and urban dwellers in developing economies (Wodon and Zaman 2009) that depend on external agricultural markets for surviving (De Hoyos and Medvedev 2011).

However, it has been proposed that several of the impacts attributed to biofuel production rely on the weak governance of developing nations to protect small landholders (Singh 2013). Several governance mechanisms—e.g., policies that promote the diversification of land production while preventing deforestation (Sawyer 2008), or the implementation of certification schemes aimed at increasing social welfare in local communities (Scarlat and Dallemand 2011)—can help to reduce the reported negative socioeconomic impacts of biofuel production in the developing world (Van der Horst and Vermeylen 2011). In the face of future increased energy and food demands, the use of non-food crops for biofuel production would be expected to reduce these impacts.

To facilitate the identification of sustainable biofuel production systems, a number of key knowledge gaps must be addressed:

i) Development and standardization of indicators (Smeets and Weterings 1999) for assessing the socioeconomic and environmental impacts of biofuel production alternatives. For biofuels, multiple indicators have been proposed in relation to soil and water quality, GHGs, air quality, and productivity (McBride et al. 2011), and in relation to social well-being, energy security, trade, profitability, and social acceptability (Dale et al. 2013). However, a more comprehensive development of some indicators, including those related to biodiversity and ecosystem services (de Souza et al. 2018, Gasparatos et al. 2018), would improve the understanding of the overall environmental impacts of biofuel production, and facilitate the assessment of biofuel production sustainability (Gasparatos et al. 2018). The standardization of indicators, which simplifies their selection and use, would benefit from the participation of stakeholders (i.e., academy, government, industries, non-governmental organizations, and communities) (Dale et al. 2017) and the understanding of the causal relationships between indicators and biophysical, socioeconomic, and governance drivers (Florin et al. 2014).

ii) Development of standardized assessments on the environmental impacts exerted by biofuel production systems. This includes the development of life-cycle assessments (LCA) that make use of the same system boundaries (e.g., well-to-wheel studies that consider cultivation, biofuel production, and final use of biofuels by consumers), impact categories, and functional units (Bradley et al. 2015). These standardized assessments would facilitate objective and measurable comparisons between different studies, as well as the development of meta-analysis on the environmental impacts of several biofuel production alternatives (Quinn and Davis 2015). For instance, Harris et al. (2015) report that there are insufficient empirical assessments to determine the impacts of second generation biofuels on GHG emissions; while Tu et al. (2017) indicate the need to harmonize assumptions, data sources, and calculation procedures in LCA, for the development of meta-analyses able to draw valid conclusions on the overall environmental impacts of microalgal production systems.

iii) Development of case studies that consider multiple socioeconomic and environmental objectives (e.g., taking into account targets in energy and food production, biodiversity conservation, and provision of multiple ecosystem services) in several locations. Techniques for identifying multiple objective solutions include multi-criteria decision analysis (MCDA) (Malczewski and Rinner 2015), multi-agent systems (MASs) (Ghadimi et al. 2017), and integer linear programming (Beyer et al. 2016). These studies require the participation of stakeholders for defining objectives, environmental indicators, criteria (Kurka and Blackwood 2013), and their weights (e.g., through analytical hierarchy process AHP) (De Lange et al. 2012). Furthermore, they would help to identify the synergies and trade-offs among objectives and criteria, for instance, between land and water requirements (Bonsch et al. 2016), between biodiversity and climate change mitigation (Hof et al. 2018), or among deforestation, CO_2 emissions, nitrogen losses, water withdrawals, and food prices (Humpenöder et al. 2018). The robustness and uncertainty of models and results can be shown through the development of sensitivity analyses (Pianosi et al. 2016). To date, several frameworks have been developed to facilitate the inclusion of multiple objectives in biofuel decision making. For instance, Zhang et al. (2010) developed a multi-objective and spatially explicit framework for biofuel production in Michigan, based on GIS, biomass yields, and trade-offs among biofuels and ecosystem services; Perimenis et al. (2011) developed a support tool for helping decision makers in selecting more sustainable biofuel production alternatives in Germany; and Garcia and You (2018) developed a framework to select the most sustainable bioethanol production alternative based global life-cycle environmental impacts (i.e., land-use change and GHG emissions) and production costs. Expanding on this work by developing detailed case studies that consider a broad range of objectives and impacts would establish an evidence-base for informing policy and planning decisions.

iv) Improved estimation of potential biofuel production at fine spatial scales, accounting for a wide range of factors that can impact both feasibility and yield (Searle and Malins 2015). Biofuel production is limited by the availability of lands for the cultivation of feedstocks (Slade et al. 2014), and the availability of the several resources involved in their production, including freshwater (Hammond and Li 2016) and nutrients (e.g., nitrogen and phosphorus) (Hein and Leemans 2012). For instance, potential global bioenergy production from wastes, including agricultural and forestry residues, would be lower compared to energy crops (i.e., 25–221 EJ vs. 22–1272 EJ y^{-1}) (Slade et al. 2014) and may be further constrained after taking into account environmental considerations for maintaining soil fertility, carbon stocks and biodiversity associated with decaying biomass (Beringer et al. 2011). The understanding of these limits and uncertainties can help decision makers choose biofuel production alternatives able to meet substantial amounts of fuel demands.

v) Development of standardized and integrated global assessments of the impacts of biofuel production considering complex socioeconomic and ecological systems (e.g., integrated assessment modeling IAM) (Liu et al. 2015). These assessments would facilitate the understanding of the complex actual and potential impacts of biofuel production alternatives at multiple spatial and temporal scales. For instance, based on the Shared Socio-Economic Pathways (SSEPs) Popp et al. (2017) suggest that high levels of bioenergy production modeled on second generation biofuels can be achieved with low impacts on ecosystems, if future demand for agricultural commodities remains low, if agricultural productivity increases, and if globalized trade is maintained.

2. Economic profitability: A current barrier to the deployment of more sustainable biofuel production systems

Economic profitability is the main barrier to the deployment of several more sustainable biofuel production systems. Currently, the lowest biofuel production costs are achieved by first generation biofuels, particularly for sugarcane bioethanol in Brazil and maize bioethanol in the USA, helped in part by government subsidies (Carriquiry et al. 2014). High costs for converting lignocellulosic feedstocks into biofuels (Carriquiry et al. 2014) and high capital and operational costs for setting up microalgal production systems (Ruiz et al. 2016), reduce the economic competitiveness of lignocellulosic and microalgal biofuel production systems. While production costs for sugarcane in Brazil and maize in the USA have been calculated at between US\$ 5–9 and US\$ 9–20 GJ^{-1}, respectively, estimated production costs for lignocellulosic feedstocks and microalgal systems (i.e., often based on assumptions about production technologies and production costs) can range between US\$ 19–62 and US\$ 13–8,949 GJ^{-1}, respectively (Carriquiry et al. 2014). For comparison, an oil price of US\$ 100 $barrel^{-1}$—a price which has only been exceeded in 20% of months in the past decade (EIA 2018)—is equivalent to US\$ 17.12 GJ^{-1} (Low Heat Value LHV). In order to be competitive, more sustainable biofuel production alternatives must approach cost equivalence with its competitors.

The cost-effectiveness of more sustainable biofuel production alternatives is expected to benefit from increased scale efficiencies and learning rates as biofuel production farms enlarge and production technologies evolve. Historical trends show significant cost reductions that several biofuel production systems—including bioethanol production from sugarcane in Brazil and from maize in the USA—have experienced as the industry matured, which is also expected to occur for more sustainable biofuel production alternatives (Daugaard et al. 2015). For second generation biofuels, the development of more cost-effective conversion technologies based on the transformation of lignocellulosic feedstocks is needed (Alonso et al. 2017). For microalgal production, the cultivation of highly productive microalgal strains (Chisti 2007) and the co-location with inexpensive CO_2 and nutrient sources (i.e., co-locating microalgal cultivation systems with CO_2 from industries and nutrients from wastewater) improve the profitability of microalgal production systems (Judd et al. 2017), particularly for open ponds (Box 7) (Slade and Bauen 2013). Reductions in production costs between 35% and 86% can be achieved if CO_2 from industries and nutrients from wastewater are obtained for free (Judd et al. 2017). Additionally, more efficient cultivation methods (e.g., using less energy-intensive mixing techniques for promoting microalgal growth) (Kumar et al. 2015), along with low-cost harvesting and de-watering methods (Slade and Bauen 2013) and the development of profitable co-products (e.g., animal feed and biogas) (Peng et al. 2018), can increase both the profitability and sustainability of microalgal biofuel production (Zhu et al. 2015). For instance, the defatted residues that remain after lipids are extracted for biodiesel production, can be used as a substrate for biogas generation and for nutrient recycling (i.e., following anaerobic digestion) (González-González et al. 2018); this biogas can either be sold or used as a source of energy and CO_2 for algae cultivation, reducing energy costs and increasing microalgal growth, while nutrient recycling reduces the dependence on fertilizers (Uggetti et al. 2014).

Box 7. Microalgal cultivation systems (open ponds and photobioreactors)

Microalgal cultivation systems include open ponds, photobioreactors, and fermenters (Zhu 2015). Raceway ponds are the most widely used type of open ponds and consist on a closed recirculation channel, built in concrete or with plastic covering the earth, usually with a depth between 15 and 30 cm, in which algae and growth medium are mixed by paddlewheels (Schenk et al. 2008). Microalgae concentrations are low, CO_2 can be added to the water for maximal productivity, and the temperature is not controlled although evaporation helps to cool the medium (Chisti 2007). Compared to photobioreactors, this system experiences higher water losses through evaporation, is less efficient in CO_2 uptake, and is more prone to contamination by other microorganisms, which results in reduced yields (Brennan and Owende 2010), but is considered a more cost-effective option for biofuel production (Slade and Bauen 2013).

Photobioreactors can consist of a series of plates, tubes, bags, columns or domes set in particular arrangements that maximize sunlight uptake. Algae concentrations are usually higher than in open ponds, the light intensity can be better optimized, the temperature can be controlled (though energy or water use increase) and CO_2 can be injected at several intervals in order to ensure continuous carbon uptake, leading to higher biomass yields than those obtained in open ponds (Schenk et al. 2008). However, setup costs may be ten times higher than those necessary for the construction of open ponds (Schenk et al. 2008), hence are considered less cost-effective to date (Slade and Bauen 2013).

Hybrid systems are based on the initial growth of microalgae in photobioreactors, avoiding contamination from other microorganisms, followed by their cultivation in open ponds (Dickinson et al. 2017) (Fig. 4).

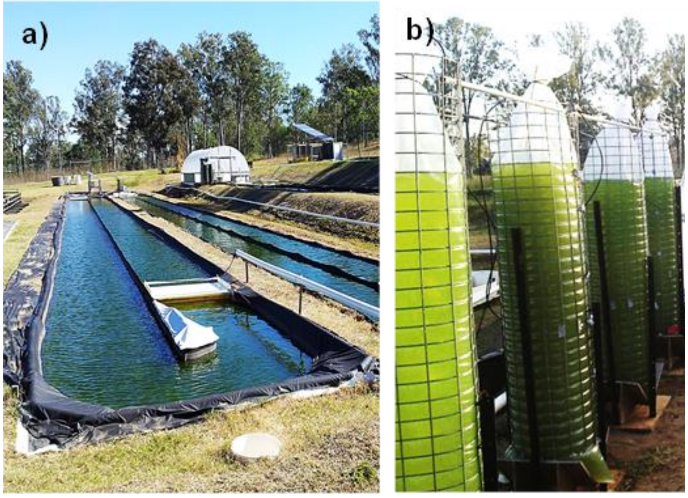

Figure 4. UQ Algae Energy Farm at Pinjarra Hills, Brisbane, Australia (Algae Biotechnology Laboratory, University of Queensland). Cultivation is based on open ponds (a) following initial growth in sealed bags and a series of smaller ponds (b).

Several strategies can facilitate the transition of transport systems based on fossil fuels and first generation biofuels to systems based on sustainable biofuels and electricity (Fig. 5) (Mathiesen et al. 2015). In the short term, the development and commercialization of high-value products can provide profits and enable scaling of production. For lignocellulosic biomass, a biorefinery system, in which value-added products such as bio-oil, biochar, and other bio-based chemicals can be produced, is expected to increase the profitability of second generation biofuels (De Bhowmick et al. 2018). Similarly, for microalgal production systems, a biorefinery-based production model (Doshi et al. 2017), in which different types of biofuels are produced (e.g., biogas and biodiesel) (González-González et al. 2018) or high-value products for food consumption and animal feed (e.g., omega-3 fatty acids, pigments, proteins, and fishmeal) are produced along with biofuels (Ruiz et al. 2016), can increase the profitability of microalgal biofuel production.

Several policies can be implemented to promote the deployment of more sustainable biofuel production systems, as has already occurred for first generation biofuels in the USA, Brazil, Europe, and other economies (Sorda et al. 2010). They include:

i) The introduction of biofuel blending mandates that require sustainable biofuel production methods, following a comprehensive evaluation of their socioeconomic and environmental benefits (Noh et al. 2016). For instance, by 2020 the European Union aims to meet 10% of total transport energy demands using renewables based on the use of biofuels that do not drive direct or indirect land-use changes in biodiverse and carbon-rich regions, and that additionally deliver GHG savings of at least 35% in comparison to fossil fuels (and from 2018, of at least 60%), considering the cultivation, processing, and transport of biofuels (EU 2015). The development of these mandates should consider synergies and trade-offs among biofuel production, socioeconomic, and environmental goals; for instance, among biofuel cultivation, restoration of degraded lands (Machovina and Feeley 2017), ecosystem services (Baumber 2017), and biodiversity conservation (Essl et al. 2018).

ii) The taxation or subsidizing of energy systems based on their environmental impacts. This would include the elimination of fossil fuel subsidies, the implementation of disincentives to less sustainable biofuels (e.g., through carbon taxation schemes) (Macaluso et al. 2018) and the subsidizing of more sustainable biofuel production alternatives while the subsidies for first generation biofuels gradually decrease (Eggert and Greaker 2014). This can boost the deployment of promising more sustainable biofuel production systems while they become economically competitive (Scarlat et al. 2015).

iii) The implementation of financial and market-based mechanisms for promoting the development of sustainable biofuel production alternatives. For instance, the use of contracts for difference (CFDs), in which biofuel producers enter a 10-year contract with governments following reverse auctions, has been proposed as a more cost-effective alternative for financing the setup of ultralow-carbon biofuels in California in comparison to capital grants (Pavlenko et al. 2017). Other mechanisms include the integration of novel and more sustainable biofuel production systems with carbon markets (Ayadi et al. 2016) and sustainability certifications schemes (Scarlat and Dallemand 2011), which can increase their profitability based on environmental advantages (e.g., reductions in GHG emissions) compared to less sustainable energy production alternatives.

iv) The development and strengthening of partnerships between governments, universities, and industries, for promoting research and innovation aimed at developing more profitable and sustainable biofuel production alternatives (Youngs and Somerville 2017).

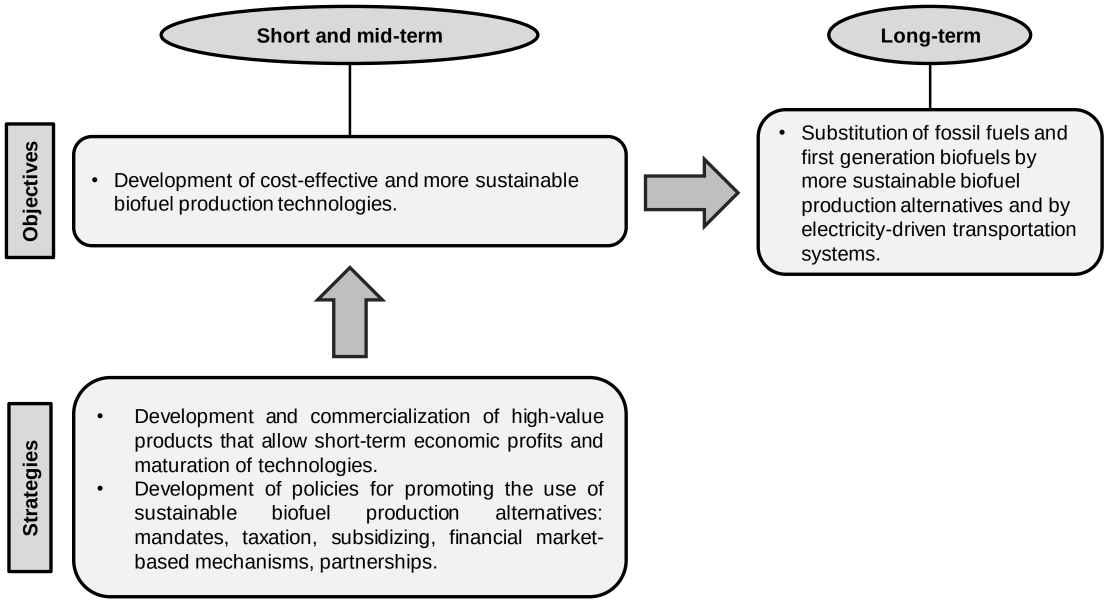

Figure 5. Strategies for promoting the implementation of more sustainable biofuel production alternatives in the short and long term.

3. Articulation of policies at the global, national, and regional level

The transition to a more sustainable transport sector can be fostered through the development of strategic policies that promote the adoption of sustainable biofuel production alternatives, able to reduce environmental impacts and halt competition with food production (Witcover et al. 2013). The articulation of policies at global, regional, national, and local scales is a necessary step for guiding the implementation of sustainable biofuels (Fig. 6). The development of an updated global roadmap on sustainable biofuels (IEA 2011), could guide nations in implementing policies in accordance with global multi-objective targets while balancing local socioeconomic and environmental needs (de LT Oliveira et al. 2017). Because the impacts of several biofuel systems are still a matter of debate, this roadmap must be subject to adjustments as new evidence on the impacts of biofuels is established (i.e., through the development of an adaptive framework on the global and local socioeconomic and environmental impacts of biofuels) (Gasparatos et al. 2013). At the global scale the biofuel industry can be supported through the development of international standards to facilitate accreditation of fuel sustainability (Scarlat and Dallemand 2011), markets to support international trade of sustainable biofuels (Proskurina et al. 2018), and trade agreements to ensure that pricing of sustainable biofuels remains competitive (Poletti and Sicurelli 2016). Furthermore, the development of international agreements based on sustainability goals (e.g., the Paris Agreement, to which most countries are signatories), provides strong incentive and justification for fostering the growth of more sustainable biofuel production systems.

National energy policy is fundamental to drive the transition to sustainable biofuels (Scarlat et al. 2015). National mandates on biofuel blends based on stringent biofuel sustainability standards (Stattman et al. 2018), can encourage the implementation of sustainable biofuels. The gradual replacement of fossil fuels and first generation biofuels can be facilitated through: (i) National-level policies that provide disincentives to fossil fuel and unsustainable biofuel production (e.g., through carbon taxation schemes) (Macaluso et al. 2018), and (ii) national-level incentive programs that promote sustainable biofuels, including the subsidizing of sustainable biofuel production, the development of financial and market-based mechanisms mediated by governments in favor of sustainable biofuels (Pavlenko et al. 2017), and the funding of applied research to develop cost-effective and sustainable biofuels (Cortez et al. 2014).

Regional level policy is critical to ensure that the growth of the biofuel industry occurs in a strategic way, avoiding biodiversity impacts, competition for agricultural land, non-sustainable use of resources (e.g., freshwater), and negative socioeconomic impacts (de LT Oliveira et al. 2017). Regional policy can also manage trade-offs among multiple stakeholders and potential conflicts among industries (Gasparatos et al. 2015), as well as help to regulate the growth of biofuels and certificate sustainable biofuels (Scarlat and Dallemand 2011).

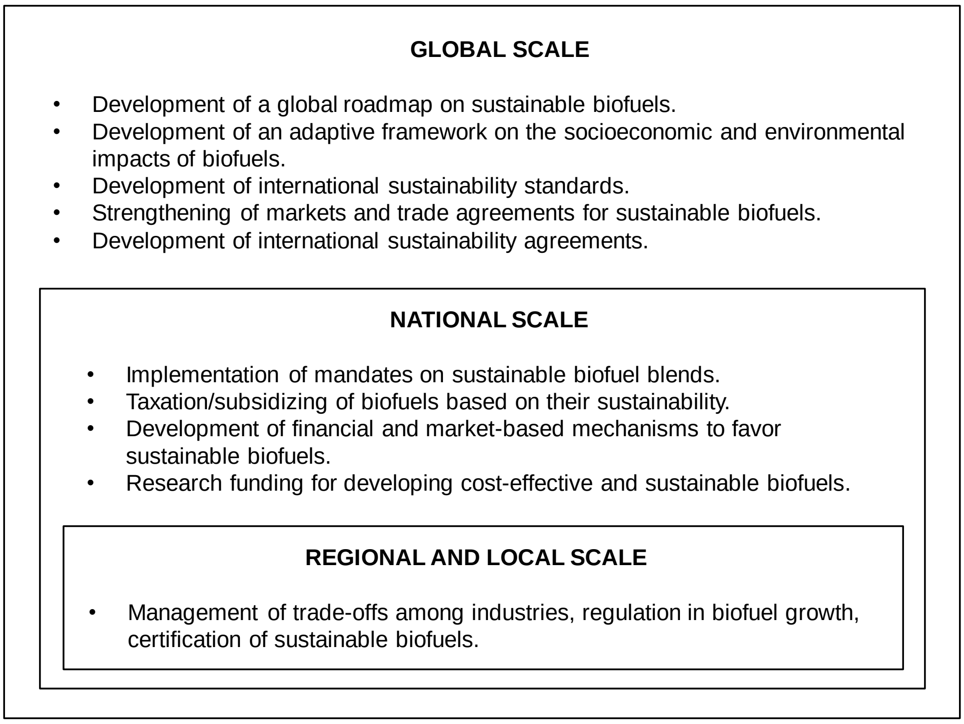

Figure 6. Articulation of policies at the global, national, regional, and local scale towards the implementation of sustainable biofuels.

4. CONCLUSIONS

Bioenergy production is expected to increase from 9.7 × 10^6 to 4.6 × 10^7 GJ d^{-1} between 2016 and 2040 (IEA 2017), and how biofuels are produced will determine their overall environmental impacts. The implementation of more sustainable biofuel production systems, which currently include sustainably sourced wastes, native perennial crop, and microalgal production systems produced on low-biodiversity or degraded lands, could reduce the magnitude of the several socioeconomic and environmental impacts exerted by first generation biofuels, mainly in terms of reduced competition with food production and biodiversity. The sustainability of these and other novel biofuel production alternatives must be carefully assessed before their widespread adoption, based on global socioeconomic and environmental targets (e.g., poverty reduction, climate change mitigation, biodiversity conservation, freshwater provision, and reduction of eutrophication). The development of robust assessments that consider the social and environmental impacts of biofuel production are needed to inform choices and implement more sustainable biofuel production alternatives. This could involve, for example, the development and standardization of environmental indicators, the development of standardized assessments on the environmental impacts exerted by biofuel production systems, the development of detailed case studies that consider multiple socioeconomic and environmental objectives, improved estimations of potential biofuel production feasibility and yield, and the development of integrated assessments to understand the socioeconomic and ecological implications of biofuel production alternatives. Technological improvements are expected to improve the profitability of more sustainable biofuel production alternatives over time, currently estimated at between US$ 19–62 for lignocellulosic feedstocks and US$ 13–8,949 GJ^{-1} for microalgal production systems (Carriquiry et al. 2014). Meanwhile, several policies (i.e., mandates, taxation, subsidizing, financial and market-based mechanisms, and applied research partnerships) can foster the development and adoption of more sustainable biofuel production systems. These policies should be articulated at the global, national, and regional levels. Third generation biofuels are a key technology for meeting long-term transport energy demands while reducing land-use changes. In Russia, India, Brazil, Canada, Mexico, Indonesia, Saudi Arabia, Iran, Australia, South Africa, and Egypt, microalgal cultivation would require less than 2% of each country's land area for fulfilling their current domestic transport energy demands.

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Chapter 5. Supplementary Information

1. Cultivation area for fulfilling transport energy demands in 2016

The following formula was used to calculate biodiesel yields per feedstock within countries. Based on Correa et al. (2017):

$$B = \frac{Y * P}{D} * 0.81$$

Where B is each country's average biodiesel yield per crop (L ha^{-1} y^{-1}), Y is each country's average crop yield between 2010 and 2017 (t ha^{-1} y^{-1}) (i.e., for food crops) (FAO 2019), P is the proportion of lipids in the seeds, D is the oil density of seeds (t L^{-1}) (Table S1), and 0.81 is the product of the assumed oil extraction efficiency (0.9) and lipid conversion efficiency into biodiesel (0.9).

For *Jatropha*, a crop yield of 5.25 t ha^{-1} was considered, based on established plantations (5 years) under irrigation (El Bassam 2010). *Jatropha curcas* can be cultivated in tropical and subtropical regions, with cultivation limits at 30 ºN and 35 ºS (Brittaine and Lutaladio 2010).

For microalgae, the 75th percentile of lipid yield estimates (L ha^{-1} y^{-1}) was calculated within each country, based on Moody et al. (2014), and then multiplied by 0.81, which is the product of the assumed oil extraction efficiency (0.9) and lipid conversion efficiency into biodiesel (0.9).

The following formula was used to calculate ethanol yields per feedstock within countries:

$$E = Y * C$$

Where E is each country's average ethanol yield per crop (L ha^{-1} y^{-1}), Y is each country's average crop yield between 2010 and 2017 (t ha^{-1} y^{-1}) (i.e., for food crops) (FAO 2019) and C is the reported conversion efficiency from crop biomass into bioethanol (L t^{-1}) (Table S2).

For *Miscanthus* and switchgrass, crop yields of 38.2 t ha^{-1} and 12.5 t ha^{-1} were respectively considered based on values obtained in the Midwest USA (Heaton et al. 2008). *Miscanthus* and switchgrass have been considered promising feedstocks for biofuel production in temperate areas (Heaton et al. 2008). For obtaining the cultivation area required to meet the total transport energy demands in 2016, the following formulas were used:

$$A = \frac{T}{B_e}$$

$$A = \frac{T}{E_e}$$

Where A is the cultivation area (ha) per crop, T corresponds to transport energy demands within countries in 2016 (GJ y^{-1}), B_e is the average biodiesel yield per crop in units of energy (GJ ha^{-1} y^{-1}), and E_e is the average ethanol yield per crop in units of energy (GJ ha^{-1} y^{-1}). Transport energy demands were converted from million tonnes of oil equivalent (MTOE) into GJ by multiplying by the conversion factor 4.1868×10^7 GJ MTOE^{-1} (IEA 2017). B_e was obtained by multiplying the average biodiesel yields B (L ha^{-1} y^{-1}) by 0.0326 GJ L^{-1} (i.e., low heating value). E_e was obtained by multiplying the average ethanol yields E (L ha^{-1} y^{-1}) by 0.0211 GJ L^{-1} (i.e., low heating value) (Hofstrand 2008).

Table S1. Seed oil percentages (El Bassam 2010) and oil densities (at 15 - 25°C) (Firestone 2013).

Crops	Seed oil percentage	Oil density (kg m^{-3})
Jatropha	37	916
Oil palm	26	920
Rapeseed	45	910
Soybean	21	919

Table S2. Conversion efficiencies for ethanol production (Correa et al. 2017).

Crops	Efficiency conversion (L t^{-1} fresh biomass)	Reference
Maize	417	El Bassam (2010), table 10.1
Miscanthus	282	Zhuang et al. (2013)
Sugarcane	83	de Vries et al. (2010)
Switchgrass	282	Zhuang et al. (2013)
Wheat	396	El Bassam (2010), table 10.1

SYNTHESIS AND CONCLUSIONS

Further environmental degradation can be halted if humanity is willing to implement more sustainable production systems (Liu et al. 2015, Griscom et al. 2017, Ripple et al. 2017). The replacement of fossil fuels by renewable energy sources is considered fundamental for limiting global warming while reaching global future energy demands (Creutzig et al. 2016, Ripple et al. 2017, Walsh et al. 2017). However, it is a challenge to identify and implement energy production systems that fulfill growing energy demands at the lowest environmental costs (Jacobson and Delucchi 2011, Creutzig et al. 2015).

This project aimed at increasing the understanding of the potential environmental impacts of microalgal biofuel production systems on biodiversity, focusing on vertebrates and comparing with food crops for biofuel production (i.e., first generation biofuels). It also aimed at determining the best locations for microalgal cultivation at global and regional scales, considering global and national current and future transport energy demands while decreasing direct competition with high-value agricultural lands and biodiverse areas. Finally, it aimed at providing considerations to identify and implement more sustainable biofuel production alternatives, including microalgal production systems, along with strategies for overcoming the current economic barriers that prevent their widespread adoption.

1. Potential environmental impacts of microalgal production systems

Liquid biofuels negatively impact biodiversity through a wide range of pressures that include direct and indirect land-use change, greenhouse gas emissions, pesticide and fertilizer pollution, water depletion, overexploitation of soils, invasive species and genetic pollution, emissions of air pollutants, and changes in factors that affect regional climate (e.g., alterations in albedo and evapotranspiration patterns). Compared to food crops (i.e., first generation biofuels), microalgal biofuel production systems could become a more sustainable biofuel production alternative, mainly in terms of reduced direct and indirect land-use change in areas with high agricultural and biodiversity value. This would result from its non-dependence on fertile soils and its higher biomass and lipid productivities per unit area. In fact, based on conservative microalgal lipid production estimates, and for producing the same amount of energy, microalgal biofuel production systems would in average need 12%, 30%, 3%, and 22% the land needed to cultivate maize, sugarcane, soybeans, and oil palm, respectively. Additional benefits include their non-dependence on pesticides (Brennan and Owende 2010, Smith et al. 2010), and reduced water usage in comparison to food crops if water is recycled (Gerbens-Leenes et al. 2014, Béchet et al. 2017).

Other pressures that directly and indirectly affect biodiversity can be reduced under the development and implementation of more sustainable microalgal production technologies. Reductions in the emission of CO_2 and air pollutants (NO_x, NH_3, CO, VOC, PM, SOx, N_2O) can be achieved through the optimization of biomass/lipid productivities per unit area (e.g., by cultivating more productive microalgal strains), the use of industrial CO_2 sources and wastewater systems, the recycling nutrients and energy (e.g., through the implementation of biorefinery systems that make use of anaerobic digesters), and the implementation of less-energy intensive processes for microalgal harvesting and lipid extraction (Slade and Bauen 2013, Mu et al. 2014, Uggetti et al. 2014, González-González et al. 2018). Risks in fertilizer pollution and spread of invasive species can be reduced by recycling water (Usher et al. 2014, Correa et al. 2017).

2. Best areas for microalgal production at global and national scales

Substantial amounts of biodiesel can be produced in human-transformed dry coasts within tropical and subtropical regions in the world. These areas offer high lipid productivities and lowest direct competition with areas of high agricultural and biodiversity value, while decreasing direct competition with scarce freshwater resources. In contrast, first generation biofuels need agricultural lands, directly competing with food production and impacting areas of higher biodiversity (Hill et al. 2006, Koh 2007, Fargione et al. 2010, Correa et al. 2017). There is a wide range in potential biodiesel production depending on several cultivation scenarios (e.g., from 5.85×10^{11} to 1.81×10^{11} L year^{-1}, representing between 17% and 6% of transport energy demands in 2016 if using fresh, brackish or salt water, or if just using seawater adjacent to known industrial CO_2 sources, respectively). Potential competition with humid areas better suited for agricultural production and with high biodiversity (e.g., Southeast Asia and Central America) could occur if fulfilling higher targets in transport energy demands by microalgal cultivation.

For satisfying domestic transport energy demands, direct competition with high-value agricultural lands and biodiverse areas would be minimal for several countries. High microalgal productivities and low competition with food production and biodiversity would occur in tropical and subtropical countries with available human-transformed dry lands compared to their domestic transport energy demands, where microalgal productivities are highest and agricultural and biodiversity value decrease. Most of these countries are located in the Middle East, Africa, and non-OECD Americas. In temperate countries, lower competition with areas of high biodiversity value is expected to occur, however, larger areas would be needed for producing the same amount of energy compared to the more productive subtropical and tropical regions.

3. Best areas for future microalgal biofuel production in Colombia, Ecuador, Panama, and Venezuela

Human-transformed dry lowlands offer the best conditions for growing significant amounts of microalgae at lowest direct competition with food production, biodiversity, and aboveground carbon storage, in contrast to first generation biofuels, which need more humid areas. Compared to oil palm and sugarcane—which are the most feasible and productive first generation biofuel production alternative in the region—microalgae would replace land-covers with lower biodiversity and aboveground biomass values (i.e., mostly croplands/natural vegetation mosaics, savannas, and grasslands, and not large areas of evergreen broadleaf forests). Furthermore, microalgal cultivation would need around half and one third the area needed by oil palm and sugarcane, respectively, for producing the same amount of energy. However, as targets in energy demands increase, microalgal biofuels would shift to more humid regions, increasing potential impacts with agriculture and biodiversity.

4. Implementing more sustainable biofuel production alternatives

Robust assessments are needed to identify and implement biofuel production systems that maximize socioeconomic and environmental benefits. This could be achieved after refining socioeconomic and environmental indicators, by developing standardized assessments (e.g., life-cycle assessments LCA) for allowing direct comparison among biofuel production alternatives, by developing case studies that consider multiple socioeconomic and environmental objectives, by improving estimations of biofuel production at fine spatial scales, and by developing assessments that integrate biofuel production systems with global socioeconomic and ecological systems. Increasing the economic competitiveness of novel and more sustainable biofuel production alternatives (e.g., sustainably sourced wastes, native perennial crops, and microalgal production systems on low biodiversity or degraded lands) compared to fossil fuels and first generation biofuels, is a current challenge. The implementation of government incentives, partnerships between government, universities and industries, and market-based mechanisms, can help to gradually replace less sustainable biofuel production systems.

5. Caveats and future work

Further robust assessments (e.g., standardized life-cycle assessments and meta-analyses) on the overall environmental impacts of microalgal biofuel production in comparison to other biofuel production alternatives are required. These assessments would need to consider several microalgal biofuel production technologies (e.g., open ponds, photobioreactors, use of anaerobic digesters, several lipid extraction routes, colocation with wastewater systems and industrial CO_2 sources, use of fresh/brackish and salt water, recycling of water) in several geographical locations (i.e., along temperate, subtropical and tropical humid and dry areas) and based on different microalgal strains, allowing a direct comparison with the environmental impacts exerted by alternative biofuel crops (e.g., food crops, perennial crops) produced in the same areas. Additional studies on costs and socioeconomic benefits of several biofuel production alternatives would facilitate the identification of optimal biofuel production systems and favor their implementation.

The refinement of further GIS analyses on optimal areas for siting microalgal production farms could benefit from the inclusion of updated databases on nutrient and CO_2 availability (e.g., considering wastewater sources and anaerobic digesters), updated databases on water availability and thresholds for water withdrawal, regional changes in labor costs and land costs, and ranges in productivity based on several microalgal strains and cultivation technologies (e.g., open ponds vs. photobioreactors). The use of updated databases on national and regional priority areas for agricultural development and biodiversity conservation can improve the selection of best areas for microalgal cultivation while decreasing direct competition with food production and biodiversity. The consideration of opportunity costs with other land-use priorities (e.g., industry, tourism, or provision of ecosystem services) can help to assess potential conflicts with socio-economic and environmental goals. Further regional and global assessments on best areas for siting biofuel production alternatives (i.e., including first, second and third generation biofuels), based on a set of global, regional, and national socioeconomic and environmental goals (e.g., targets in biofuel blends, food production, biodiversity conservation, carbon storage, provision of water), can guide decision making for optimal multi-objective land-use planning.

Engaging with stakeholders involved in biofuel production, environmental protection, and policy development, can facilitate the identification and implementation of profitable and sustainable biofuel production systems. These systems should be able to meet socio-economic and environmental goals at local, regional, and global scales. The integration of views from biofuel producers can guide the development of socio-economic goals towards the adoption of profitable and equitable biofuel production alternatives, while the integration of views from the environmental sector can guide the development of systems that offer fewer environmental impacts or that improve the quality of the environment and ecosystem services. Finally, the participation of policy makers can facilitate the adoption of these sustainable biofuel production systems. Sharing the results of the thesis with bioenergy production stakeholders can promote the identification and adoption of more sustainable biofuels.

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