Effects of bioenergy on biodiversity arising from land-use change and crop type

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Impact Statement: Meta-analysis reveals that replacing natural ecosystems with bioenergy crops across the planet will largely be detrimental for biodiversity.

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Abstract

Understanding how the world's flora and fauna will respond to bioenergy expansion is critical. This issue is particularly pronounced considering bioenergy's potential role as a driver of land-use change, the variety of production crops being considered and currently used for biomass, and the diversity of ecosystems that can potentially supply land for bioenergy across the planet. We conducted a global meta-analysis to ask how eight of the most commonly used bioenergy crops may impact site-level biodiversity. Species diversity and abundance were generally lower in crops being considered for bioenergy when compared to the natural ecosystems they may replace. First-generation crops, derived from oils, sugars, and starches, tended to have greater effects than second-generation crops, derived from lignocellulose, woody crops, or residues. Crop yield had non-linear effects on abundance and, to a lesser extent overall biodiversity, with biodiversity effects being driven by negative yield effects for birds but not other taxa. Our results emphasize that replacing natural ecosystems with bioenergy crops across the planet will largely be detrimental for biodiversity, with first generation and high yielding crops having the strongest negative effects. We argue that meeting energy goals with bioenergy using existing marginal lands or via biomass extraction within existing production landscapes may provide more biodiversity friendly alternatives than via land conversion of natural ecosystems.

Introduction

Ever-increasing global demand for energy is associated with a diverse portfolio of sustainable energy options, and bioenergy has been championed as an especially promising choice (OECD-FAO 2017). Biofuels and bioenergy are thought to be sustainable energy options because they can reduce carbon emissions, provide habitat and ecosystem services, and decrease reliance on fossil fuels (Fargione et al. 2010; but see Searchinger et al. 2008). As a consequence, bioenergy production is expected to increase significantly in many parts of the world in the coming years (OECD-FAO 2017).

Increased bioenergy demand can be met, at least partially, with existing residual biomass sources, thereby avoiding potential harm to native ecosystems (Lal 2005). However, increased bioenergy production has led to conversion of natural ecosystems close to refineries and is expected to continue to drive direct and indirect land-use change (Havlik et al. 2011; Koh 2007; Koh & Wilcove 2008; Lambin & Meyfroidt 2011, Wright et al. 2017). Because bioenergy has the greatest footprint, in terms of land requirements per unit of energy of all energy sources (McDonald et al. 2009; Trainor et al. 2016), land-use change resulting from efforts to increase bioenergy production could impact ecosystems in a variety of ways (Groom et al. 2008; Bradshaw et al. 2009; Edwards et al. 2010; Dauber and Bolte 2014; Immerzeel et al. 2014; Burton et al. 2017). In particular, there is increasing concern that biodiversity may be affected.

Nonetheless, the effects of increased bioenergy production on biodiversity and ecosystems across the planet remain unclear. For example, when analyzing crop production scenarios, high-yield crops are often predicted to have greater impacts to biodiversity than low-yield crops (Green et al. 2005; Koh et al. 2009; Anderson-Teixeira et al. 2012; Law et al. 2017; but see Klein et al. 2002), but there are few tests of this expectation. Similarly, first-generation bioenergy crops (derived from oils, sugars, and starches; e.g., corn ethanol), which often compete for land with food production, are thought to have greater impacts to biodiversity than second-generation bioenergy crops (derived from lignocellulose, woody crops, or residues; e.g., *Pinus* sp.; Havlik et al. 2011, Immerzeel et al. 2014). Further, second-generation crops often come from otherwise unused sources of biomass such as residues from forestry operations or from prairies, from which biomass harvest is often compatible with wildlife conservation (Fargione et al. 2009, 2010; Fletcher et al. 2011). Local studies along with regional and crop-specific meta-analyses have illustrated the potential impacts of bioenergy on biodiversity (e.g., Koh & Wilcove 2008; Fletcher et al. 2011; Verschuyl et al. 2011; Robertson et al. 2012; Werling et al. 2014; Gottlieb et al. 2017). However, currently there has been no attempt to quantitatively synthesize these problems related to bioenergy and impacts to biodiversity across the planet (but see Immerzeel et al. 2014 for qualitative global review). A global view is needed because it provides a means to interpret the wide variety of scenarios being considered, which vary greatly in the types and potential yields of crops, local biodiversity, and how different types of bioenergy production strategies (e.g., first versus second generation) may impact biodiversity. A quantitative meta-analytic framework provides an objective means to test for the generality of potential effects of bioenergy on biodiversity, which has proven difficult with non-quantitative methods (Immerzeel et al. 2014).

We provide the first global meta-analysis on the potential impacts of bioenergy crops on biodiversity. To do so, we conducted two global literature searches: one directed at finding data on biodiversity in different production land uses, and another aimed at extracting energy yield estimates of potential bioenergy crops. We then tested whether effects on biodiversity varied with different individual bioenergy crop species (henceforth, crop type), estimated energy yield, first or second-generation crops, the type of reference ecosystem considered (i.e., forest, shrub, or grassland ecosystems), and magnitude of vertical change in habitat structure between any given crop and the reference ecosystem (see section on hypothesis rationale). We expected that effects may increase with energy yield (Anderson-Teixeira et al. 2012), effects would be greater for first generation rather than second generation crops (Havlik et al. 2011, Immerzeel et al. 2014), and effects would be greater as the structural differences of bioenergy crops and reference ecosystems increased (Fletcher et al. 2011).

Methods

Building a global dataset for biodiversity and bioenergy crops

We searched for articles that quantified components of biodiversity in landuses relevant to bioenergy production, and in natural habitats such landuses may replace. Using a combination of keywords *biodiversity* and *biofuels* along with each crop using the operator word “AND” (e.g., *biodiversity* AND *eucalyptus, biofuels* AND *eucalyptus, biodiversity* AND *jatropha, biofuels* AND *jatropha*, etc.), we searched in June of 2019 for published articles that studied biodiversity and the main bioenergy feedstocks being considered in the future or currently used throughout the world. These were corn (*Zea mays*), eucalyptus (*Eucalyptus oblique*), jatropha (*Jatropha curcas*), oil palm (*Elaeis guineensis*), pine (*Pinus spp.*), poplar (*Populus spp.*), soybean (*Glycine max*), sugarcane (*Saccharum officinarum*), and switchgrass (*Panicum virgatum*) (Fargione et al. 2010; OECD-FAO 2017). We also searched for 'rowcrops' and included studies that pooled results from more than one type of row crop (primarily corn and soybean, which are frequently rotated; West and Post 2002). Of the 2334 articles considered, we identified 147 articles that compared components of biodiversity in at least one candidate bioenergy crop with a reference land use, which entailed a natural (e.g., forest ecosystem) or low-intensity (e.g., pasture) land use (Figures 1, 2), and had results written in English, Spanish, Portuguese, Italian, or French (Figure 1, Table S1 and S2). It is possible that these search terms may have not captured all relevant papers on the topic. However, based on the total number of studies included in our study, we assume our search returned a representative sample of relevant papers.

Because of the newly emerging bioenergy economy, there are very limited data that provide time series regarding land-use change from bioenergy and resulting changes in biodiversity. Here we use space-for-time substitution to interpret potential bioenergy effects by contrasting biodiversity in crops that have been proposed or currently used for bioenergy paired with data from natural ecosystems that may be vulnerable to conversion to bioenergy crops, such as grasslands being converted to bioenergy crops (e.g., switchgrass or corn; Wright & Wimberly 2013). This approach has been used previously for interpreting effects of bioenergy alternatives (Fletcher et al. 2011; Meehan et al. 2010; Riffell et al. 2011). Note here that we pooled variation within crops (e.g., pine plantation ages), which can potentially mediate bioenergy impacts on biodiversity (see, e.g., Riffell et al. 2011; Gottlieb et al. 2017). Furthermore, some investigations were not contrasting lands currently used for bioenergy production, but rather studying biodiversity in the major crops being considered for bioenergy that were producing other products at that time (e.g., timber, food; Fletcher et al. 2011). Focusing solely on lands used exclusively to produce bioenergy would be useful because biomass extraction for bioenergy could lead to subtle differences in land use relative to the same crops being used for other purposes. However, given that many of these crops are just beginning to be commercially produced for bioenergy, it was not possible to restrict our search in this manner.

We then searched for articles that quantified energy produced from different bioenergy crops. We searched on July 21st, 2015 using a combination of keywords *biofuels* and *biomass* along with each crop using the operator word “AND”: *eucalyptus, jatropha, oil palm, pine, poplar, soybean, sugarcane, row crop,* and *switchgrass*. Some crops (e.g., corn and sugarcane) can potentially be used as a biomass source for second-generation bioenergy as well. To account for uncertainty of yields, changes in expected yield over time, and literature search date, we also considered maximum yield reported for each crop. To delineate each crop as a first or second-generation bioenergy crop, we followed Fargione et al. (2010) and crop use predictions from FAO-OECD (2015). We found 3074 studies that were published between 1987 and 2015. From those studies we extracted 280 values for either biomass or energy values of the selected crops. Selected studies were either individual field trials or studies that synthesized data from previous trials. To provide a useful basis for comparison and analysis, out of the 280 selected yield values, 41 were converted from biomass units (e.g., Mg/Ha/Yr) to bioenergy units (GJ/Ha/Yr) and 16 were converted from amount of liquid biofuel (e.g., L/Ha/Yr) to bioenergy units (see Supplementary Materials for details).

How bioenergy crops may impact biodiversity: rationale and testing

We tested two sets of predictions to address how bioenergy crops may impact biodiversity. The first set contained predictions related to attributes of bioenergy crops and the second set tested predictions related to attributes of natural ecosystems.

To test possible effects of different attributes of bioenergy crops on biodiversity, we tested three main predictions. First, the *yield hypothesis* states yields drives biodiversity effects, predicting an inverse relationship between the two (Green et al. 2005; Phalan et al. 2011; Phalan et al. 2016). In some cases, yield is implicitly assumed to be a proxy for land-use intensity to represent the amount of output (e.g., food) that an area can produce (Green et al. 2005; Phalan et al. 2011). Therefore, crops with different land-use intensity and yield can alter habitat differently, affecting biodiversity by increasing the strength of these effects as yield of crops increases (i.e., land-use intensity increases). Moreover, given the breadth of global biodiversity and how different species might react differently to changes in land use (Devictor et al. 2008), we assessed if this relationship was linear or non-linear (i.e., quadratic or logarithmic). We also considered a logarithmic relationship because of potentially greater effects on biodiversity per unit change in yield occurring at low yields than at high yields (Green et al. 2005; Phalan et al. 2011). This could be because at higher yields the landscape may have already affected biodiversity (e.g., by reducing or fragmenting critical habitat) and therefore, a unit increase in yield might affect biodiversity only marginally. To test this prediction, for each bioenergy crop we included the average energy yield value, which we derived from the literature search on energy yield. Also, we considered two other approaches to interpreting yield effects by considering maximum reported yield and a bootstrap approach. We made these choices because crop yields increased over the last 50 years, they are expected to continue to increase (Pretty et al. 2006; Aizen et al. 2008; OECD-FAO 2017), and there is uncertainty in yield estimates. Both of these approaches provided similar conclusions (See Supporting Information).

Second, the *biofuel-generation hypothesis* states that crop generation drives biodiversity impacts, with second-generation crops influencing biodiversity less than first-generation crops (Immerzeel et al. 2014). Some second-generation crops can offer similar ecosystem attributes to natural environments (e.g., the use of switchgrass in the mid-western U.S., a native grass in the region; Fargione et al. 2010; Fletcher et al. 2011). Finally, the *crop-type hypothesis* states that crop type drives biodiversity impacts. In this scenario, each crop affects biodiversity independently of yield and generation, because of specific crop characteristics (e.g., rotation cycles, water or fertilizer requirements; Kremen 2015).

The second set of predictions relate to natural ecosystems that may be replaced under bioenergy production. The *ecosystem-type hypothesis* suggests that biodiversity impacts are driven by the type of original ecosystem replaced on the landscape. Under this hypothesis, when forested ecosystems are replaced for bioenergy, the impacts to biodiversity may be different in comparison to when shrubland or grassland ecosystems are replaced. This difference is expected based on average differences in species richness among these ecosystem types (Ricklefs & Schluter 1993; Tilman & Pacala 1993). The *dissimilar land-use hypothesis* suggests that similarity of biofuel crop type to the native landscape drives biodiversity impacts. If correct, then replacing a natural ecosystem with a bioenergy crop that provides similar vegetation structure impacts biodiversity differently than when natural ecosystems are replaced with crop of dissimilar vegetation structure. This prediction states that land-use changes from bioenergy crops with greater differences in structure to reference ecosystems would lead to greater negative effects (Foley et al. 2005; Laliberte et al. 2010).

To test these predictions, we used two approaches. First, we classified each reference ecosystem in a study into forest and shrubland or grassland sites (i.e., "reference structure"). Second, we qualitatively assessed the magnitude of vertical change in vegetation structure between any given crop and a natural ecosystem (as a proxy for dissimilar land-use) into three categories of relative contrast: lower, moderate, and higher. Lower magnitude of change included (reference-crop) forest-woody crop, grassland-pasture, shrubland-pasture comparisons. Moderate magnitude of change included grassland-row crop, shrubland-woody crop, and shrubland-row crop. Higher magnitude of change included forest-pasture, forest-row crop, and grassland-woody crop comparisons. It is possible that factors related to bioenergy crops together with attributes of natural ecosystems that are being replaced for bioenergy production might be driving biodiversity impacts. To test this relationship, we built models with additive effect of main predictions related to crops and natural ecosystems.

Analyzing the global dataset

We contrasted estimates of species abundance (either abundance or density) or diversity (species richness or diversity metrics, e.g., Shannon's index) between potential bioenergy crops and reference sites (Fletcher et al. 2011). We excluded crops in cases where we only found ≤ 3 studies (e.g., jatropha, diversity metrics for switchgrass). These studies yielded 5191 pair-wise comparisons for abundance and 313 for diversity. Our effect size was the log response ratio (i.e., $\ln[(X_{bioenergy}+1)/(X_{reference}+1)]$; Hedges et al. 1999; Fletcher et al. 2011; Lajeunesse 2015). We built generalized linear mixed models (GLMM) using effect sizes as response variables. Lajeunesse (2015) suggests a way to adjust for inter-study variability based on the study's reported standard error. However, many studies failed to report measures of uncertainty (e.g., SEs, CIs), which prevented us from following the method proposed by Lajeunesse (2015). To control for potential sources of variability emanating from different studies, we adjusted relative contribution of each study by weighting the effect size with the number of replicates in potential bioenergy stands and reference ecosystems ([($N_{(\text{bioenergy crop})} \times N_{(\text{Reference habitat})}$)/(($N_{(\text{bioenergy crop})} + N_{(\text{Reference habitat})}$)]; Adams et al. 1997; Mosqueira et al. 2000; de Graaff et al. 2006, Hammon et al. 2018), and included each study as a random effect in all models (i.e., we "blocked" all observations that emanated from each study; Bender et al. 1998; Bates et al. 2015). To control and test for potential differences arising from each taxon, we built two sets of GLMMs. In the first set, we pooled data from all taxa and added a random intercept effect for each taxon (results in Table S4). In the second set, we modeled each taxon separately (results in Table S5-S9).

Using model selection, we then tested how effect sizes varied with different individual bioenergy crop type, estimated energy yield, first or second-generation crops, the type of reference ecosystem considered (i.e., forest, shrub, or grassland ecosystems), and magnitude of vertical change in habitat structure between any given crop and the reference ecosystem. We tested for these effects pooled across all taxa and separately for different taxonomic groups (birds, mammals, invertebrates, reptiles and amphibians, and plants) and built a total of 151 models to include all taxa and predictions tested. We did not consider some tests for specific taxon when data precluded it; for example, when testing for yield effects, we only fit models when effect sizes were measured for at least 4 different yields. We ranked each model that tested a hypothesis based on Akaike's information criterion, adjusted for small sample sizes (AICc) and interpreted models within <2 AICc from the top model. We considered models with lowest AICc the most parsimonious. All modeling was done in program R (R Development Core Team 2008) using the package "lmer" for building GLMMs (Bates et al. 2015), and package "MuMIn" for model selection (Bartoń 2009). We infer significant effects based on the 95% CIs for parameters from models.

Results

Overall, biodiversity tended to be lower in bioenergy crops relative to reference natural ecosystems: metrics of diversity (e.g., species richness) were significantly lower, whereas abundance on average was lower but confidence intervals overlapped zero (Figure 2 and S2). Sixty-four percent of abundance and 72% of diversity effect sizes found negative impacts on biodiversity. Every taxon considered showed negative effects of bioenergy on diversity; for abundance, insects and birds showed significant negative effects, plants and amphibians and reptiles showed negative, but not statistically strong effects, while mammals showed positive effects of bioenergy on abundance (Figure 2). The positive effects on mammal abundance was largely driven by data on non-native mammals, mostly invasive species, in pine plantations in Argentina. When considering biomass crops, we found significant negative effects of oil palm, Eucalyptus, row crops, and pine on diversity metrics, whereas, oil palm had negative effects on abundance metrics (Figure 3).

Effects on biodiversity metrics were best explained by whether crops were first-generation or second-generation feedstocks and the reference land-use considered (Figure 4 and Table S4). First-generation crops tended to show greater negative effects on biodiversity than second-generation crops generation crops. These effects were largely observed in birds and plants in comparison with mammals, reptiles, amphibians, and invertebrates (Figure S2). When considering reference ecosystems, impacts on biodiversity were greater when comparing forested to grassland ecosystems (Figure 4 and S2). Yield of crops was relevant for diversity responses only for some taxa. Our results show that bioenergy crops with high biomass yield hold less bird diversity than low-yielding bioenergy crops (β = -0.29, 95% CI: -0.29 – -0.28; Figure 5; see Table S5 for parameter estimates for top performing models). The strongest negative effect on birds was recorded from oil palm. However, we did not find strong statistical evidence to support a relationship between energy yield of bioenergy crops and diversity of plants or invertebrates (Figure 5). For mammals, and the group composed of reptiles and amphibians, yield was among the top performing models together with the null model (Table S6)

Effects on abundance metrics were best explained by the yield of crops, but a model considering whether crops were first-generation or second-generation feedstocks and the reference land-use considered was also supported (Table S4, Figure 4 and 5). Impacts on species' abundance was greater as crop yield increased, (β = -0.15, 95% CI: -0.15 – -0.16; Figure 5; for parameter estimates for top performing models see Table S4). This effect was more evident for birds in comparison to other taxa (Figure 5 and S2). As with diversity, impacts on abundance of species were strongest when comparing bioenergy crops to forested ecosystems and for first generation crops (Figure 4).

Discussion

Bioenergy is often considered a potential sustainable energy alternative and an increase in bioenergy production across the planet is expected in the coming years (Fargione et al. 2010, OECD-FAO 2017). Our results showed that in most cases, abundance and diversity may be negatively impacted from land conversion of natural habitats. Importantly, we also show that impacts may be more severe with first generation (e.g., corn) than second generation crops, high yielding crops, and when forest is converted to crops. These results can provide guidance to inform policy and land management strategies that aim to minimize impacts to biodiversity.

Bioenergy, land-use tradeoffs and biodiversity

Tradeoffs between agricultural production yields and impact to biodiversity are often emphasized in agro-ecology, conservation biology, and sustainability science (e.g., land sparing vs land sharing; Green et al. 2005; Phalan et al. 2011; Fischer et al. 2014; Kremen

2015; Phalan et al. 2016). For bioenergy production, there has been emphasis on developing high-yielding biomass crops that may require less land for a target energy goal (Heaton et al. 2008). Yet, empirical data on such relationships remain limited (but see, e.g., Kleijn et al. 2009; Phalan et al. 2011) and potential tradeoffs have not been tested for the problem of bioenergy and biodiversity. We found evidence for negative effects of crop yield on bird biodiversity. However, unlike in some other studies focused on food production (Kleijn et al. 2009; Phalan et al. 2011), we did not find strong evidence for consistent effects of crop energy yield on biodiversity across all taxa (Figure 2 and Table S4). Given that our analysis focuses on some crops also used for food production, these results have broad relevance to understanding land-use biodiversity tradeoffs in a context of increased food and energy demand.

Despite general negative effects of bioenergy crops on biodiversity (Figure 2), we detected relatively weak effects based on yield, first generation versus second generation feedstocks, and reference land-use. At least three reasons might explain this lack of strong effects. First, site-specific conditions can moderate the effects of potential bioenergy crops. For instance, favorable environmental conditions in pine plantations could have driven higher abundance and richness, especially for invasive species (Liu et al. 2012) and in well-managed plantations (e.g., Gottlieb et al. 2017). Heterogeneous landscapes with hedgerows or forest patches and ecological traits that allow some species to thrive in agriculture can explain high diversity and abundance in sugarcane, soybean, and corn (Minor and Cianciolo 2007; Mulwa et al. 2012; Nunes et al. 2006; Nuñez-Regueiro et al. 2015). Studies showed that higher abundance and diversity in poplar and oil palm plantations relative to native forest can be explained by the presence of generalist species (Edwards et al. 2013; Martin-Garcia et al. 2013). Second, life-history strategies and management schemes for different crops may play a larger role on biodiversity effects than yield alone. Yield has been often used as a proxy of land-use intensity across the land-sharing vs land-sparing spectrum

(Green et al. 2005; Phalan et al. 2011, 2016) and arguably measures other than crop yield could be more useful to understand ecological tradeoffs (Klein et al. 2002). Bioenergy crops differ greatly in energy balances and production schemes, such as rotation, agrochemical inputs, and socio-economic contexts (Farrel et al. 2006; Koh et al. 2008; Kremen 2015; Zhu et al. 2017). Third, the sample size of studies across crop types varied considerably, which impacts the power of interpreting effects for some crops. Sixty-nine percent of the literature focused on forested biomass sources. Conversely, only 16% included row crops that may have a greater impact on biodiversity due to intensive crop management strategies and structural simplicity, such as soybean and corn (Tables S2 and S3, Fletcher et al. 2011; Robertson et al. 2012; Gottlieb et al. 2017). Similarly, because of low number of studies published for some crops, our data set included only eight bioenergy crops. This focus on a small number of crops may have reduced our statistical power and potentially hid yield-biodiversity relationships. Yield-biodiversity tradeoffs may become more apparent as data from more crop systems and taxa increase (Kremen 2015).

While these results provide a much-needed quantitative comparison among bioenergy crops being considered and used throughout the world, our search also revealed major data gaps for understanding the impacts of bioenergy. We found very limited (or no) information on some key bioenergy crops (e.g., jatropha, switchgrass), and some taxa were poorly represented. Furthermore, there was apparent geographic bias in the articles we found, with limited work in the southern cone of South America (Argentina, Bolivia, Chile, Paraguay and Uruguay), north east Asia (northern China, Mongolia, and Russia), and in most countries in Africa (with the exception of southern Africa) (Fig. 1).

Implications for Conservation

Our results point to the accumulating evidence that land conversion of natural ecosystems for bioenergy production will likely have negative impacts (Fletcher et al. 2011, Imerzeel et al. 2014). While some crops showed greater changes than others (Fig. 3), the general pattern of lower diversity and abundance was clear. These results emphasize that policy and management strategies that aim for sustainable bioenergy production should provide mechanisms to avoid land conversion in native ecosystems. While some existing policy has such directives (US-EPA 2010), land-use change near bioenergy refineries has been documented (Wright et al. 2017), suggesting that policy mechanisms may not be sufficient to minimize wholesale land change.

Our results and other recent findings suggest at least three ways to reduce impacts. First, crop type can minimize or exacerbate effects, depending on crop yield and whether crops are first or second generation. Second, some potential impacts can be mitigated based on the ways in which biomass is extracted from existing land uses (e.g., Vershuel et al. 2011, Gottlieb et al. 2017). For instance, bioenergy can be produced from residue biomass or from biomass grown on degraded and abandoned lands without converting natural ecosystems (Fargione et al. 2008). Third, land-use change that may arise from bioenergy production wherein more intensive agriculture is replaced by bioenergy crops, which could have net benefits to biodiversity (e.g., converting row crops to second-generation bioenergy land-uses). For example, replacing annual row-crops with perennial bioenergy crops like switchgrass could benefit local biodiversity (Werling et al. 2011; Meehan et al. 2012), assuming no indirect land-use change due to decreased food production. Fourth, landscape composition and configuration of surrounding farms also can affect biodiversity (Robertson et al. 2011; Karp et al. 2018; Miljanic et al. 2019) and can moderate potential effects of bioenergy.

Conclusions

One of humanity's greatest challenges is balancing food production, energy production, and protection of the environment (Tilman et al. 2001). Bioenergy crops that do not compete with food production and require smaller footprints (i.e., have high energy yields) have been championed as a way to help meet this goal (e.g., Heaton et al. 2008). However, there remain ongoing concerns regarding potentially greater environmental impacts with higher yield crops (Anderson-Teixeira et al. 2012). Nonetheless, in the next 20 years bioenergy will likely still be largely produced from sources like corn or soybeans (OECD-FAO 2017). This expectation is mainly because of slow development of technologies to achieve large production scales of high-yielding crops at competitive prices (OECD-FAO 2017). Our results highlight the consequence to biodiversity when attempting to meet production goals using first-generation crops (see also Immerzeel et al. 2014). We show that, even when including characteristics of natural environments, yield is an important factor driving impacts to biodiversity, although its effect varies across taxa. Furthermore, our results suggest that replacing natural ecosystems to produce bioenergy will largely harm biodiversity. Bioenergy and land-use policies that protect remaining natural habitat from conversion to energy crops will be critical to achieve biodiversity conservation goals in conjunction with renewable transportation fuel goals.

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Figure Captions

Figure 1. Country-level summary of studies included in our meta-analysis (pie charts represent the proportion of bioenergy crop studies per country and number of studies in each country is shown on top of each pie chart) and bioenergy production increase by 2024 (% increase in production) for the expected top 10 largest bioenergy-producing countries (data from OECD-FAO 2016). Panels (a) through (g) show land cover examples for each potential bioenergy crop

Figure 2. Estimated impacts of replacing reference ecosystems with potential bioenergy crops on the world's flora and fauna. Impacts are calculated as the amount of biodiversity (diversity and abundance) in bioenergy croplands relative to reference ecosystems (log response ratio). Data points left of the zero vertical line signal less biodiversity in bioenergy crops than in reference ecosystems and thus represent an impact on biodiversity. For example, a value of -0.5 on the x axis signals that approximately for every 3 species or individuals detected in bioenergy crops, 5 species or individuals are detected in reference ecosystems. Error bars represent 95% confidence intervals.

Figure 3. Estimated global impacts of replacing reference ecosystems with potential bioenergy crops. Impacts are calculated as the amount of biodiversity (diversity and abundance) in bioenergy croplands relative to reference ecosystems (log response ratio). Data points left of the zero vertical line signal less biodiversity in bioenergy crops than in reference ecosystems and thus represent an impact on biodiversity. For example, a value of -0.5 on the x axis signals that approximately for every 3 species or individuals detected in bioenergy crops, 5 species or individuals are detected in reference ecosystems. Error bars represent 95% confidence intervals.

Figure 4. Estimated global impacts of replacing grassland or forest ecosystems with first or second generation bioenergy crops. Impacts are calculated as the amount of biodiversity

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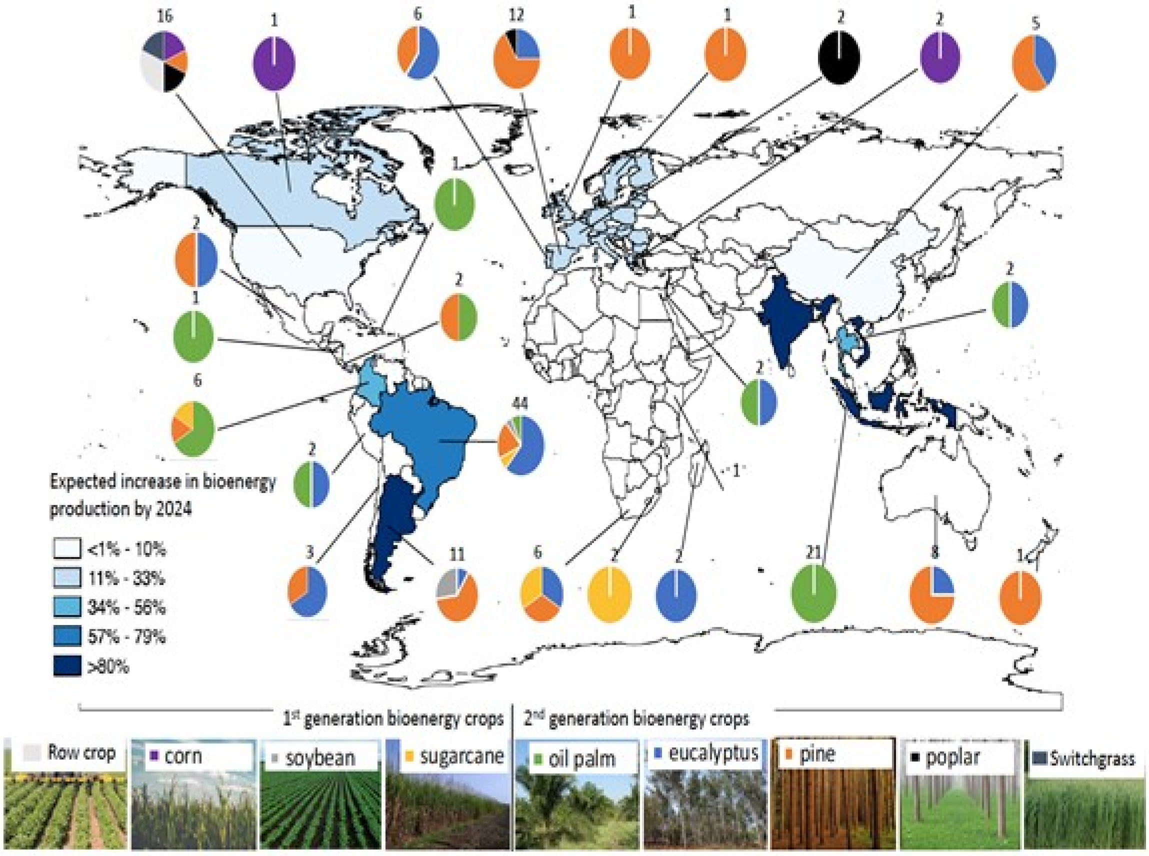
Figure 5. Estimated global impacts of replacing reference ecosystems with potential bioenergy crops of varying energy. Impacts are calculated as the amount of biodiversity (diversity and abundance) in bioenergy croplands relative to reference ecosystems (log response ratio). Data points below the zero horizontal line signal less biodiversity in bioenergy crops than in reference ecosystems and thus represent an impact on biodiversity. (a) and (b) show results pooled for each taxa for abundance and diversity data, respectively across all bioenergy crops. Below the horizontal line at zero (0), biodiversity in bioenergy crops is less than in reference ecosystem. For example, a value of -0.5 on the x axis signals that approximately for every 3 species or individuals detected in bioenergy crops, 5 species or individuals are detected in reference ecosystems. Error bars and colored areas represent 95% confidence intervals.



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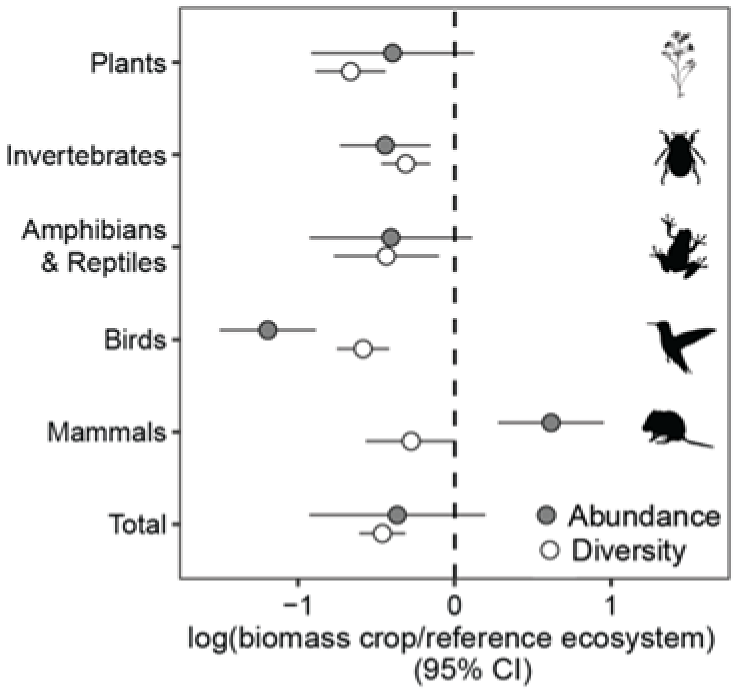

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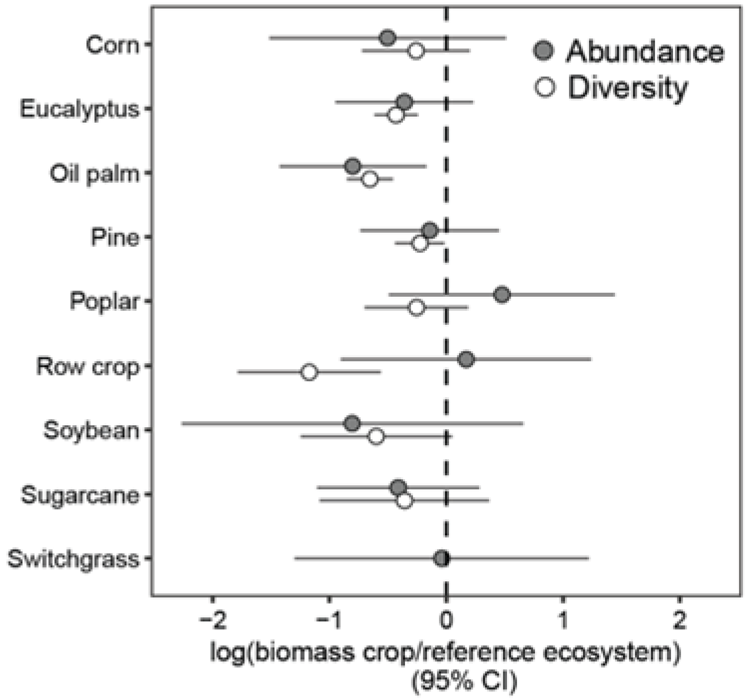
Fig. 3



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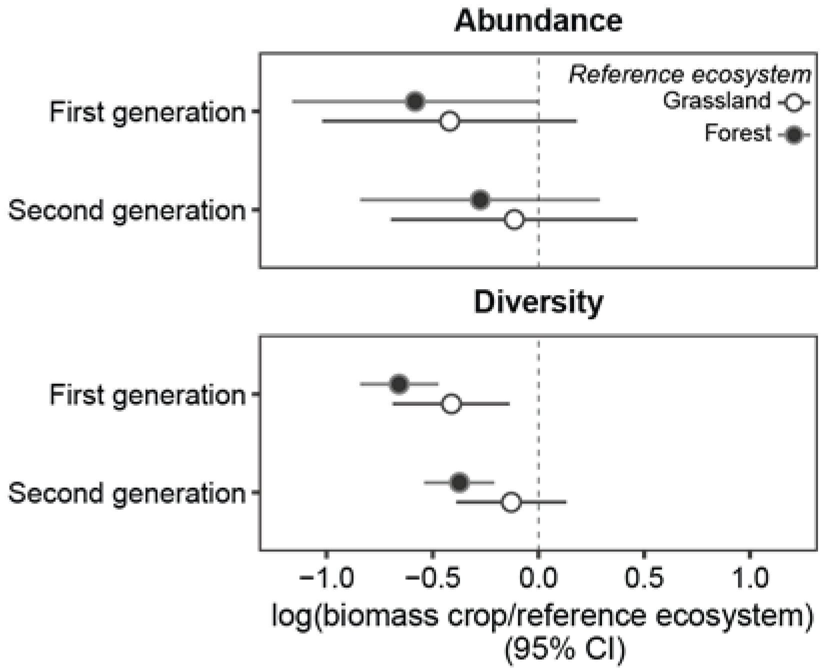

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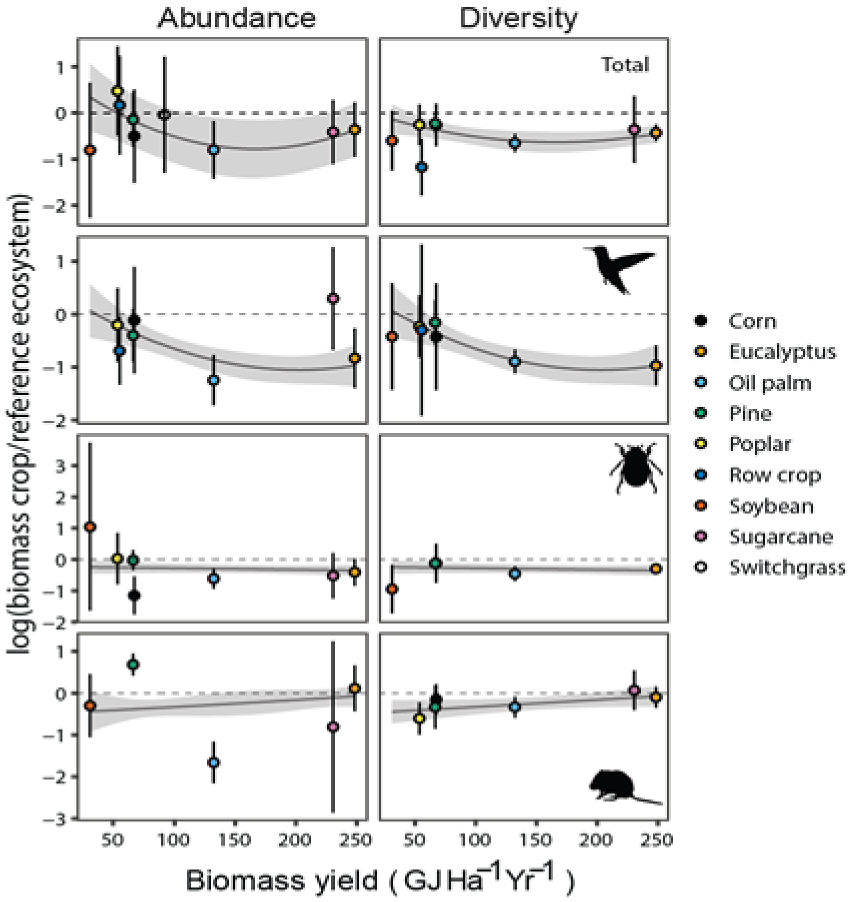

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