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Biological control protects carbon sequestration capacity of plantation forests

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With 2 figures and 3 tables

Abstract: In many natural and managed forest and tree systems, pest attacks and related dieback events have become a matter of increasing global concern. Although these attacks modify the carbon balance of tree systems, their contribution to climate forcing and the relative impact of nature-based mitigation measures is seldom considered. Here, we assess the extent to which biological control protects or reconstitutes carbon sequestration capacity and storage in monoculture tree plantations globally. Specifically, we draw upon field-level assessments, niche modeling and forest carbon flux maps to quantify potential risk of carbon sequestration loss due to three globally important insect herbivores of pine and eucalyptus. Specifically, herbivory by the tree-feeding insects *Sirex noctilio, Leptocybe invasa* and *Ophelimus maskelli* conservatively reduces carbon sink capacity by up to 0.96–4.86% at the country level. For a subset of 30, 11 and nine tree-growing countries, this potentially compromises a respective 4.02%, 0.80% and 0.79% of the carbon sink capacity of their tree hosts. Yet, in the invasive range, released biological control agents can help regain lost sink capacity to considerable extent. Equally, across both the *S. noctilio* native and invasive range, carbon sequestration capacity is protected by resident biota to the tune of (max.) 0.28–0.39 tons of CO_2 equivalent per hectare per year. Our exploratory valuation of pest-induced sequestration losses and their biodiversity-driven mitigation informs climate policy, biosecurity, and management practice.

Keywords: biocontrol; climate change; invasion biology; plantation forestry; restoration ecology

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1 Introduction

Natural and man-made forests represent a carbon sink equivalent to up to 22% of anthropogenic emissions (IPPC 2019), thus assuming a critical role in the global carbon cycle and efforts to mitigate climate change (Pan et al. 2011). While natural forests' superiority over forest plantations in terms of contribution to biodiversity and ecosystem services is well established, forest plantations are here to stay (Horak et al. 2019; Lewis et al. 2019; Du et al. 2022). For instance, nearly 45% of recent high-level forest restoration pledges entail the establishment of commercial tree monocultures; a hallmark feature of plantation forestry worldwide (Nichols et al. 2006; Hurley et al. 2016). Given the outlook of forest plantation expansion, it is critical to understand the impact of pests on tree health and specifically their capacity to deliver ecosystem services such as carbon sequestration. While natural forests hold larger carbon stocks per se and ensure stable, reliable carbon capture, short-cycle tree plantations exhibit higher carbon accumulation rates (Horak et al. 2019; Bukoski et al. 2022). Indeed, forest plantations demonstrate substantial carbon sequestration potential, with some systems storing up to 214 tonnes of C ha^{-1} (Kongsager et al. 2013), while properly managed production forests could increase sequestration capacity by approximately 20% (Domke et al. 2020). Time-averaged carbon storage in planted forests can reach 40–80 tonnes of C ha^{-1} in living trees and 70–90 tonnes of C ha^{-1} in soil organic matter (Dewar & Cannell 1992), contributing significantly to national carbon offset goals, with forests and harvested wood products offsetting more than 14% of economy-wide CO_2 emissions in some countries (Domke et al. 2020). This sequestration capacity is particularly evident in fast-growing exotics such as *Eucalyptus* spp., which sequester above-ground carbon at 127% the rate of native species across geographies and production contexts (Bukoski et al. 2022).

Coniferous tree plantations (including pine, *Pinus* spp.) cover over 80 million ha whereas eucalyptus is planted on 22 million hectares globally (Poyry 1999). In South America alone, more than 5 million hectares of pine are grown (Medina-Torres et al. 2022). Fiber or pulp tree plantations are regularly managed as short-cycle, economically-driven rotations (Curtis et al. 2018; Table 1), and involve cultivating tree species outside their native range. Thus, high biomass growth rates of exotic tree plantations are often ascribed to a so-called 'enemy release' hypothesis in which exotic species thrive at their introduced locations due to an absence of many or all of the herbivores and pathogens that may impact them within their native range (Brockerhoff & Liebhold 2017). This effect declines as the previously lost "enemies" (i.e., exotic pests) arrive and native herbivores expand their host range for instance due to climate change (Flory & Clay 2013; Wingfield et al. 2015; Ghelardini et al. 2017; Gougherty & Davies 2022). One new herbivorous insect species now arrives every 1.4 years in eucalyptus plantations worldwide (Hurley et al. 2016) and the number of pests in the non-native range of *Eucalyptus* spp. far surpasses that in its native range (Gougherty & Davies 2022). These involve various sap-suckers, defoliators, gall formers and wood borers, several of which have spread extensively since their initial detection (Hurley et al. 2016). Those pests cause diffuse mortality to tree plantations and compromise ecosystem service delivery (Flower & Gonzalez-Meler 2015). In particular, non-native pests severely impact carbon accumulation where they benefit from 'enemy release' from their arthropod or microbial natural enemies (Gandhi & Herms 2010).

Insects and pathogens increasingly affect tree-based systems and the frequency, severity and spatial coverage of pest-induced damage is a matter of mounting concern (Kautz et al. 2017; Fei et al. 2019). In the USA, forests, insect and disease attacks lower carbon sequestration by a respective 69% and 28% in live trees as compared to that in plots with no recent disturbances (Quirion et al. 2021). Comparatively small sets of forest pests cause tree mortality rates on the order of 5.5 million tonnes (Mt) of C per year in the USA (Fei et al. 2019) and threaten 1,027 Mt of live tree C in European forests (Seidl et al. 2018). Outbreaks of the mountain pine beetle *Dendroctonus ponderosae* have shifted the forest carbon balance by up to 20 Mt of C per year in British Columbia, equivalent to 75% of Canada's annual forest fire emissions (Kurz et al. 2008). Lastly, pathogens have recently led to extensive mortality of *Castanea, Cercis* and *Tsuga* tree genera in parts of North America (Anderson-Teixeira et al. 2021). As such, both native and exotic pests and pathogens transform forest demographics, alter successional trajectories and derail carbon cycling (Millar & Stephenson 2015; McDowell et al. 2020). Those impacts attain scales and magnitudes comparable to climate forcing, but only receive scant scientific attention (Flower & Gonzalez-Meler 2015) and have only been assessed effectively in selected temperate settings.

These processes can be moderated either by restoring ecological balance through a scientifically guided introduction of (selective) predatory or parasitoid natural enemies from the native range (i.e., classical biological control; Hoddle 2004; Van Driesche et al. 2010; Kenis et al. 2019) or through the natural regulation of herbivore populations in their native range (i.e., natural biological control; Estes et al. 2011; Xu et al. 2023). Yet, even in the case of natural biological control, it often involves planted forests that are established outside of the native range. The latter process is particularly important as it safeguards photosynthetic capacity at a planetary scale (Hairston et al. 1960). Yet, regardless of the critical role of tree plantations in the global carbon cycle, the impacts of either form of biological control on carbon sequestration remain unquantified.

In this study, we combine field data with ecological niche modeling and forest carbon flux maps to estimate the impact of biological control on carbon sequestration in eucalyptus and pine plantations. First, we identify the climatic range of each tree herbivore (or 'pest') through maximum entropy modeling based upon its global occurrence records (Phillips et al. 2006). Next, we overlay the boundaries of pine and eucalyptus plantations in selected countries (Du et al. 2022) with maps of forest carbon flux (Harris et al. 2021). Assuming that the impacts of a given pest on carbon sequestration increase near linearly with its climatic suitability (Flower & Gonzalez-Meler 2015; Koontz 2021) without accounting for primary host resource amounts (Root 1973) or environmental parameters, we estimate the possible shortfall in carbon sequestration for each pest across its potential range. Lastly, we assess how either form of biological control protects or reconstitutes carbon sink capacity by contrasting the projected losses between areas where the pest is under (natural) biological control versus those where such option is not (yet) available. After an exhaustive discussion of data gaps and shortcomings in our exploratory modeling effort, we end by calling for increased attention to biological control in global forest management.

2 Materials & methods

2.1 Target tree-pest systems

Among the hundreds of invasive arthropod pests and pathogens of global tree plantations, we focus on three insect herbivores that are of particular interest outside of Western nations because of their area coverage, severity of attack and potential carbon impact (Table 1). The sirex wood wasp (*Sirex noctilio* F.) (Hymenoptera: Siricidae) is an invasive wood-boring pest of pine trees native to the Palearctic. Feeding damage of *S. noctilio* larvae and an associated decay fungus cause extensive mortality in invaded areas (Cameron et al. 2018; Kenis et al. 2017b). The gall wasps *Leptocybe invasa* Fischer & La Salle and *Ophelimus maskelli* (Ashmead) (Hymenoptera: Eulophidae) are native to Australasia, but have colonized eucalyptus stands on other continents since 2000 (Hurley et al. 2016). In affected stands, both species cause heavy galling, leaf curling and severe growth disruption. In their native range, all three herbivores are variably kept at bay through natural biological control, though competition and host effects are also important. In parts of the invaded range, classical biological control has been extensively used (Kenis et al. 2019). Classical biological control is especially well suited as a management option for invasive pests; by restoring the ecological balance of invaded ecosystems, it provides long-lasting, efficacious control at high returns on investments (Kenis et al. 2017a). However, though the target herbivores and associated natural enemies have been comparatively well studied, there is a paucity of information on their implications for tree C exchange or storage.

2.2 Occurrence records

Occurrence records for the three target herbivores or pests i.e., *S. noctilio, L. invasa* and *O. maskeli* were obtained from the following sources: 1) scientific publications in which details are provided on the geographical distribution or occurrence of a given species; 2) online distribution databases from CAB International (CABI) and the European Plant Protection Organization (EPPO); 3) open-access databases with species-level occurrence data from the Global Biodiversity Information Facility (GBIF). For *S. noctilio*, the above data were complemented with a geospatial database comprising 69 individual locations from the United States and Canada (Evans et al. 2016), in which the centroid of a given county was used for county-level records and point location were used for reports with more accurate e.g., county-level information. For each pest-level occurrence record, country, state or province data were extracted and the latitude/longitude records were entered into a spreadsheet. Next, we plotted occurrence records using Google Map and created keyhole markup language (KML) files. We then visualized the (tentative) distribution of each pest based upon the available set of occurrence records using ArcMap software (ESRI, Redlands, California, USA).

Table 1. Aboveground carbon accumulation rates and pest-induced impacts for eucalyptus and pine plantation crops. Carbon sequestration rates are indicated as average values (and maxima) over different rotation lengths expressed in tonnes of C ha^{-1} yr^{-1}. For each of the tree genera, we also list the common duration of economically-driven rotations or economic lifespan. For a given pathogen or pest, we provide damage-related indices e.g., growth reduction, stunting, tree mortality, defoliation, field-level incidence that are reported in the global literature.

Tree species	Carbon accumulation rate[1]	Rotation length (yr)[2]	Pest	Impact indices	Ref.[3]
Eucalyptus spp.	7.8 (max. 23.8)	5–15	*Ophelimus maskeli*	>90% reduction in Dbh[4] increment Extensive leaf shedding	1, 2
			Leptocybe invasav	7.8% reduction in Dbh increment 6.3% reduction in tree height 44.4% trees (very) severely damaged	3, 4
Pinus spp.	1.9 (max. 9.4)	10–18	*Sirex noctilio*	Tree mortality 0.5–5.0% per year	5, 6

[1] Bukoski et al. 2022. [2] Kanninen 2010. [3] References listed in Supplementary Table S1. [4] Diameter at breast height.

2.3 Ecological niche modeling

Climate-based niche modeling was conducted using the Maximum Entropy method (MAXENT; Phillips et al. 2006), in which climatic suitability values are generated based upon (pest) occurrence records, pseudo-absences and an array of bioclimatic variables. The Maximum Entropy model compares favorably to models that use presence-only data such as GARP, Bioclim and Domain (Busby 1991; Carpenter et al. 1993; Stockwell & Peters 1999; Hernandez et al. 2006). More so, machine-learning toolkits such as MAXENT generally outperform some of the more established modeling approaches, especially where data are noisy or sparse (Elith et al. 2006). For the five pests, availability of limited (occurrence) data for cross-validation restricted the number of model runs to 10 iterations. An equal number of pseudo-absence and presence records was used for each pest (Bunn et al. 2015; Castro-Llanos 2019).

Model development consisted of a four-step process and was replicated for each of the five forest pests. First, occurrence records for each target pest were accessed and 19 different bioclimatic variables, as averaged over 1970–2000, were drawn from the WorldClim database (version 2.1; Fick & Hijmans 2017). This database offers accurate, up-to-date climatic data including precipitation, maximum average and minimum temperature at a resolution of 2.5 arc minutes or approx. 5 km. Second, we removed any duplicates i.e., records that co-occurred within a 10-km distance in order to eliminate (spatial) bias. Third, in order to eliminate overfitting and thus reduce bias in the forthcoming results, we used the variance inflation factor (VIF) index and eliminated highly correlated variables (Warren & Seifert 2011). Values of the bioclimatic variables were extracted and those with high multicollinearity i.e., surpassing a threshold value of 10 (Marquardt 1970) were identified in the correlation matrix and eliminated from the modeling exercise. Lastly, we removed any presence data with atypical climatic values that are possibly ascribed to faulty GPS recordings or transcription errors.

Model development used 75% of occurrence records for model training and 25% of data points for validation. To evaluate overall model performance i.e., ability to discriminate between presence and absence, we relied upon metrics such as the area under the curve (AUC) (Hernandez et al. 2006). AUC values below 0.7 indicate poor ability to discriminate pest presence from randomly generated pseudo-absence, while a 0.7–0.9 range reflects moderate performance and values above 0.9 indicate high, reliable performance. Upon selection of a high-performing niche model, we assessed spatial coincidence of each pest and its plantation (host) tree species, either from known locations or potential ranges based on spatial modeling. Lastly, for each of the retained niche models and bioclimatic variables, we conducted a sensitivity analysis as per Castro-Llanos et al. (2019).

2.4 Pest-induced carbon sequestration loss

For the (cultivated) host tree crops of the three target pests i.e., fine-resolution boundaries of pine and eucalyptus plantations were extracted from the Spatial Database of Planted Trees (SDPT) of the World Resources Institute (WRI; Harris et al. 2019). This database was developed by compiling and synthesizing national or regional data, and provides the global spatial distribution of planted forests and tree crops with information on tree species. Although the current version of SDPT does not cover all countries and regions of the world, it is gradually being optimized and expanded as an active database. Accessible through the Google Earth Engine (GEE) platform, this database is based upon a global map of planting years of plantations (Du et al. 2022) and covers approx. 90% of plantation forests globally as compared to FAO's Forest Resources Assessment 2020 (FAO 2020). Specifically, SDPT reports almost 264 million hectares of planted forest while FAO reports 293 million hectares (Jessica Richter, personal communication). For each target pest, plantation boundaries were thus accessed for multiple species, sub-species or varieties of its host trees e.g., Japanese black pine, Korean pine, Korean red pine, pitch pine, shortleaf pine, slash pine or loblolly pine for *S. noctilio* (Supplementary Table S2). Boundary selection was done using selection criteria and verification protocols specified by Du et al. (2022). Boundaries were merged for all relevant host tree taxa and WRI classifications, and selected classifications were validated using aerial photography or panoramic street views on Google interfaces. Baseline maps were generated through time-series Landsat archive data over 1982–2020 using the LandTrendr algorithm (Du et al. 2022), and generated as grid cells at a 30-m spatial resolution. Using the GEE platform, masks of plantation areas of each host tree species were then overlaid on the 30-m resolution carbon sink capacity (CSC) data that have been developed based upon global forest change data since 2000 (Hansen et al. 2013; Harris et al. 2021). Emission factors, carbon fluxes and overall CSC estimates were derived from in-situ measurements of above ground biomass. Maps thus include carbon loss due to deforestation, carbon sequestration through tree growth and net carbon exchange (Harris et al. 2021).

Next, in order to estimate pest-induced changes in carbon exchange for a panel of five pests and four plantation tree crops, we entered the following equation in GEE:

$$CSL = CSC - \left[CSC \times \frac{S - T}{S_{max} - T} \times MM\right]$$

where *CSL* is the carbon sequestration loss through a pest-induced reduction in tree growth or development; *CSC* is the carbon sink capacity or sequestration rate (tonnes of CO_2 yr^{-1}) based upon satellite-derived carbon flux maps as per Harris et al. (2021); *S* is the Maxent climatic suitability score for a given pest at a particular location; T is the Maxent threshold value below which the climate is deemed unsuitable for the pest; and MM is maximum impact of a given pest on the year-by-year development or growth parameters of its host tree, based on estimates available in the global literature. Impact metrics – expressed as the annual percentage reduction in increments of trunk diameter (diameter at breast height; Dbh), tree height, leaf shedding or overall tree mortality – differed between pests and their associated plantation tree species (Table 1). In particular, MM was calculated by multiplying maximum field-level incidence by annual pest-inflicted tree mortality or growth reduction as per Table (1) without accounting for the extent to which early-season mortality can be compensated through replanting. For instance, in young (1–3 yr old) eucalyptus plantations, the impact of *O. maskelli* and *L. invasa* gall-makers causes up to 92% growth reduction (Table 1) but heavily infested plantlets are routinely replaced. Hence, for this particular tree x pest couplet, we used a conservative measure of 1% tree mortality per annum across all tree ages. Given the challenge to accurately gauge the impact of some biota, those metrics served as proxies of the extent of pest-induced changes in carbon sequestration or net carbon flux for a specific plantation tree species. Based upon Maxent model outputs, we used 0.84, 0.82 and 0.96 or 0.41, 0.40 and 0.49 as respective S_{max} or T values for *S. noctilio, O. maskelli* and *L. invasa*. We thereby assume that a pest such as *S. noctilio* (potentially) causes 84% mortality in areas where it attains ~100% climatic suitability, this while discounting the role of resident competitors, predators, environmental variables or host plant resistance. As (locality-specific) data on intra-specific host susceptibility to a given pest are routinely absent, we further assumed that all pine species irrespective of stand age, stocking levels or plantation management were uniformly susceptible to *S. noctilio* and all Eucalyptus species proved similarly susceptible to *L. invasa* or *O. maskelli*.

The above equation was implemented pixel-by-pixel through GEE and built upon locality-specific data on 1) combined satellite-derived and ground-truthed measurements of carbon sequestration through tree growth in a particular plantation; 2) actual presence of or climatic suitability for a given pest; and 3) an approximation of pest-induced reductions in tree growth or survival within a particular pest x tree system. Potential pest-induced loss in carbon sink capacity i.e., CSL was expressed in tonnes of CO_2 per year, computed in absolute and relative terms at varying spatial grain. To facilitate future interpretation, potential sink capacity loss was translated into more relatable terms i.e., annual emissions from passenger vehicles, using the Greenhouse Gas Equivalencies Calculator of the US Environmental Protection Agency (EPA).

2.5 Biological control impacts

Lastly, we visualized the foregone or restored sink capacity loss, through the action of resident natural enemies (i.e., natural biological control) in the pest's native range and sporadically also in its invasive range, or through a (deliberate, fortuitous) introduction of non-native agents (i.e., classical biological control) in its invasive range. Here, we contrasted the potential CSL (on a per-area basis) between countries where either of the three insect herbivores is native or invasive, and those where it is deemed to cause economically-relevant losses or not e.g., due to previous or ongoing control efforts (Table 2). By doing so, we accounted for the eventual contribution of endemic parasitoids in the invasive range as is the case for *S. noctilio* in North America (Slippers et al. 2015). To differentiate impacts between the two forms of biological control, the above data were intertwined with country-level records on historical biological control introductions and the ensuing impacts of introduced agents (Table 2).

2.6 Limitations of the analytical approach

Our study has limitations. First, the current plantation extent dataset by Du et al. (2022) lacks plantation boundary data for multiple key pulp- or fiber-tree producing countries. Evidently, in the absence of digitized plantation maps for specific countries, it is impossible to gauge the local carbon impact of specific pests or mitigation measures. Projections are specifically constrained by the absence of production figures for pine e.g., in Canada, China, Chile, Scandinavian countries or Russia (Zhao et al. 2020) or for eucalyptus in China, Nigeria, Paraguay, the Maghreb region or the Middle East. Lack of such data prevents forecasting the carbon sequestration impact of invasive pests in unaffected plantations e.g., for *S. noctilio* in Japan (Slippers et al. 2015) and may thus hamper biosecurity efforts. Our projections are equally constrained by an inability to geographically differentiate tree growth or carbon sequestration impacts between a pest's region of origin – where pest populations are kept at bay through the action of resident natural enemies (Hoddle 2004) – and its invasive range. This particularly applies to eucalyptus pests given the absence of plantation data from Australasia i.e., the native range of *Eucalyptus* spp. Additional challenges are the poor delineation of the geographic origin of most pests and the existence of multiple strains with varying origin, interbreeding, microbial associates and the associated variability in growth rate or feeding impact (Slippers et al. 2015; Gevers et al. 2021). Third, our calculations do not account for inter- or intra-specific variability in tree susceptibility to pest attack (Nyeko et al. 2007), the occasional multi-species or -hybrid mixed plantations (Hurley et al. 2016) or impacts that are closely tied to host tree phenology. For instance, the gall-makers *L. invasa* and *O. maskelli* primarily affect eucalyptus in young plantations or at the nursery stage (Mendel et al. 2004; Dhahri et al. 2010). Lastly, we cannot assess how pest-host tree interplay is mediated by environmental parameters including climate change e.g., with drought or warmer temperatures routinely favoring pest population build-up (Gely et al. 2020; Robbins

Table 2. Distributional range of the three selected forest pests, with an in-depth view onto the geographical extent and relative success of classical biological control introductions that have been made over the past century. Only the primary biological control agents (BCAs) used and those that have been reported to have established in their introduced range are listed.[1] Based on countries included in Fig. 2.[2] Only the primary BCAs used and those that have been reported to have established in their introduced range are listed.[3] References listed in Supplementary Table S1.

Pest	Native range of pest[1]	Introduced BCA[2]	Countries where BCAs introduced (intentional or unintentional)	Extent of pest suppression by BCAs in introduced range[3]
Sirex noctilio	Austria, Belgium, Cyprus, Denmark, France, Germany, Greece, Hungary, Italy, Portugal, Romania, Serbia, Spain	*Deladenus siricidicola, Ibalia leucospoides, Megarhyssa nortoni*	Argentina, Australia, Brazil, Canada, Chile, China, Eswatini, New Zealand, South Africa, Uruguay, USA	– Up to 90% (New Zealand; Zondag 1979) – Up to 80% (Brazil; Iede et al. 1998)
Leptocybe invasa	Australia	*Quadrastichus mendeli, Selitrichodes kryceri, S. neseri*	Argentina, Brazil, Cambodia, China, Eswatini, India, Israel, Italy, Laos, Malawi, Mauritius, Rwanda, Thailand, South Africa, Vietnam, Zimbabwe	– Up to 70% (South Africa; Gevers et al. 2021)
Ophelimus maskelli	Australia	*Closterocerus chamaeleon*	Algeria, Argentina Chile, Colombia, Ethiopia, Indonesia, Israel, Italy, Portugal, Sicily, South Africa, Spain, Tunisia, Turkey, USA	– Mean of 41% (Israel; Protasov et al. 2007) – Mean of 63% (Portugal; Branco et al. 2009) – Above 65% and up to 100% (Sicily; Caleca et al. 2011) – Up to 90% (South Africa; unpublished data)

et al. 2022). These environmental effects are partially mirrored in the 10-fold variation in *S. noctilio*-induced tree mortality between invaded settings and may engender complex feedbacks through disruptions of the global carbon sink (Mahecha et al. 2022).

3 Results

For *S. noctilio, O. maskelli* and *L. invasa*, we located a total of 1425, 415 and 620 occurrence records, respectively (Fig. 1; Supplementary Table S3; Supplementary Table S4). Climate-niche models show good performance: AUC values ranged between 0.84 and 0.99, with the lowest values for *L. invasa* (Supplementary Fig. S1). In the best-performing models for each pest, between 6 to 9 variables were retained while avoiding correlated variables. Variables with strong relationships with pest distributions include bio_9, mean temperature of the driest quarter (*S. noctilio*); bio_14, precipitation of the driest month (*O. maskelli*), bio_19, precipitation of the driest quarter (*L. invasiva*) and bio_8, mean temperature of the wettest quarter (*O. maskelli*). Climatic suitability maps accurately reflect the global distribution of each pest, as indicated by its occurrence records (Fig. 1; Supplementary Table S3). The three best-performing models exhibited a high performance with AUC values between 0.9 and 1, indicating that modeled presence data do not follow a randomized pattern (Supplementary Fig. S1). Profile analysis further reveals to what extent increases in specific bioclimatic variables affect overall model suitability i.e., mirroring model robustness or sensitivity (Supplementary Fig. S2).

For *S. noctilio*, its actual distribution corresponds with climate-based niche maps in most places where climates are moderately or highly suitable. Overall, high suitability is indicated at high latitudes in the USA, Canada, parts of the European continent, western parts of Russia and isolated areas in the Americas including in southern Brazil, eastern Argentina, Mexico, the Caribbean and the Andes. For *L. invasa*, our best model indicates suitability in India, China, southern Brazil, northern Argentina and throughout Mesoamerica. For the second eucalyptus gall-wasp, *O. maskelli*, models indicate high climatic suitability in the Mediterranean and Western Europe, southern parts of Africa, the west coast of USA and southern Australia.

Based on plantation boundaries compiled from online databases, our plantation maps cover 134,318 km^2; 165,200 km^2 and 121,606 km^2 of the primary tree hosts for *S. noctilio, L. invasa* and *O. maskelli*, respectively. For *S. noctilio*, tree cover maps included data from 30 different countries worldwide. Plantation coverage data for *Eucalyptus* spp. were less comprehensive given that only 11 and nine countries were included in *L. invasa* and *O. maskelli* modeling exercises. The above pests experienced suitable condi-

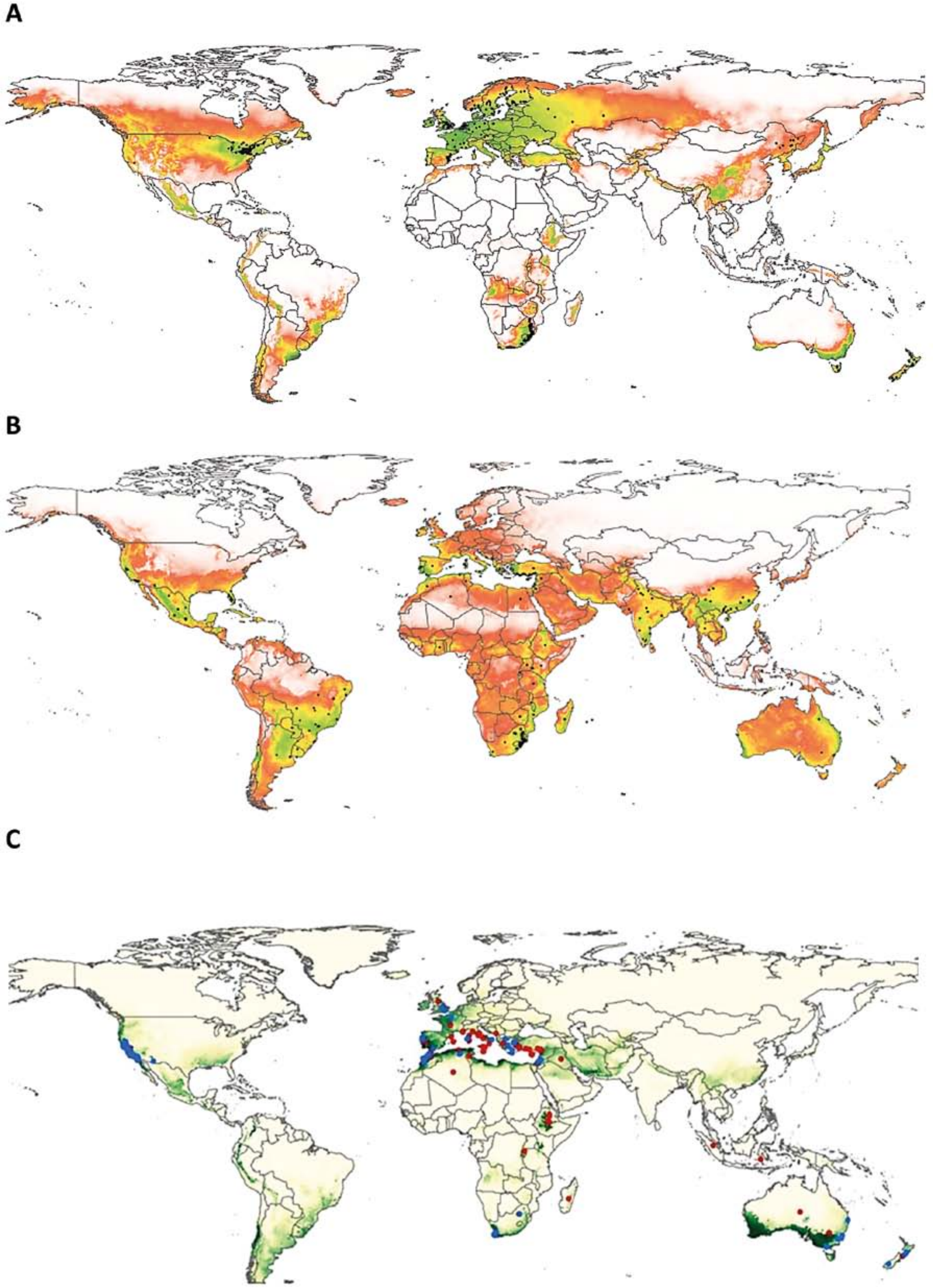

Fig. 1. Climatic suitability maps for three globally important insect herbivores of tree plantations, as generated through maximum entropy modeling. Maps depict results of climate-based niche models for *S. noctilio* (A), *L. invasa* (B) and *O. maskelli* (C). Occurrence records for each species are overlaid on its respective suitability map, and shown with dots of varying color depending upon the exact data source (Supplementary Table S4). For each species, a color gradient mirrors the extent of climatic suitability up to a species-specific maximum i.e., darkest hue.

tions on a respective 73.9%, 51.7%, 42.3% of total plantation area (Table 3). In those climatically-suitable areas, pine and eucalyptus monocultures were estimated to sequester carbon at rates of 56.6, 120.3 or 27.2 million tonnes of CO_2 equivalent per year. Across geographies, our estimated values for potential pest-induced carbon sequestration loss ranged from 0.79% for *O. maskelli* and 0.80% for *L. invasa* to 4.02% for *S. noctilio* (Table 3). For *S. noctilio, L. invasa* and *O. maskelli*, the (potentially) foregone carbon sequestration in all territories for which plantation data were available was equivalent to the annual emissions of 506,461; 215,362 and 47,771 gasoline powered passenger cars.

For most countries that have been invaded by *S. noctilio, L. invasa* or *O. maskelli*, classical biological control has reconstituted this carbon sink capacity (Fig. 2). This practice may have restored carbon sequestration rates by up to 0.15 (Argentina) to 0.16 (Brazil), 0.02 (Italy) to 0.22 (Brazil), and 0.01 (Italy) to 0.12 (Brazil) tonnes of CO_2 equivalent per ha per year, respectively. In countries where classical biological control remains to be implemented, carbon sequestration capacity could be restored to the respective tune of up to 0.09 (India, Republic of Korea), 0.02–0.07 (Japan, Pakistan) and 0.04–0.06 (Burundi, Rwanda) tonnes of CO_2 equivalent per ha per year. Meanwhile, natural biological control protects sink capacity in the pests' native range and ensures its partial reconstitution in *S. noctilio* affected areas of North America. Its impacts for *S. noctilio* ranged from up to 0.05 (Slovakia) to 0.39 tonnes (Slovenia) of CO_2 equivalent per ha per year while no data are available from the native range of *L. invasa* and *O. maskelli*. Lastly, in the USA, the action of endemic parasitoids against the locally invasive *S. noctilio* protects up to 0.28 tonnes of CO_2 equivalent per ha per year in susceptible pine plantations.

4 Discussion

Pest and pathogen outbreaks have a major impact on tree cover (Millar & Stephenson 2015; McDowell et al. 2020) and their role in climate forcing may be similar in magnitude to wildfire (Flower & Gonzalez-Meler 2015; Kautz et al. 2017; Fei et al. 2019). In this study, we provide a first approximation of the extent to which biological control offsets such pest-induced sequestration losses in selected plantation monocultures at the country level. By combining niche models with global carbon flux maps, we estimate that *S. noctilio, L. invasa* and *O. maskelli* lower carbon sequestration by a respective 2.3, 1.0 and 0.2 million tonnes CO_2 equivalent per year in 30, 11 and nine countries. These estimates are conservative and lower than the carbon sink capacity losses due to pine beetle outbreaks in British Columbia (Kurz et al. 2008). These potential pest-induced losses are variably offset through biological control (classical or natural), with a protection or reconstitution of carbon sink capacity up to 0.22–0.39 tonnes of CO_2 equivalent per ha per year across focal pests and geographies. Yet, given the paucity of plantation boundary data, our projections comprise less than 35.8% and 55.2–75.1% of global cultivation areas for pine and eucalyptus (FAO 2001). Regardless of these shortfalls, our findings are vital for climate policy, biosecurity, and tree plantation management globally – providing orders of magnitude and likely hotspots for reduced terrestrial carbon uptake.

Our findings emphasize the importance of ground-truthing for gauging pest impacts and the efficacy of resident or released biological control agents. In European and North American forests, inventory plots have lent reliable insights into the scale and magnitude of pest impacts (Anderson-Teixeira et al. 2021; Quirion et al. 2021), yet such fine-

Table 3. Potential carbon sequestration loss (CSL) in plantation tree monocultures due to three insect herbivores, in the absence of biological control. Projections are based upon climate-based environmental suitability or impact metrics for each pest species, as overlaid on carbon flux maps for its primary plantation tree hosts in selected countries. Specifically, for *S. noctilio, L. invasa* and *O. maskelli*, carbon sequestration loss (CSL) is modeled for a respective 30, 11 and nine countries. Per herbivore species, a varying set of host tree taxa and classifications is included (Supplementary Table S2). For each tree-pest couplet, we report gross carbon sink capacity (CSC) of the host tree plantations in the absence of the pest and (absolute, relative) pest-induced CSL. Sequestration loss is estimated at smaller spatial grain for the three most impacted countries, though can be (partially) neutralized through biological control in the pests' native or invasive range alike (Fig. 2).

Target pest	Affected area ('000 ha)	Gross CSC (Gg CO_2e yr^{-1})	Pest-induced CSL (Gg CO_2e yr^{-1}; %)	Top countries (potential absolute loss; Gg CO_2e/yr)	Top countries (potential relative loss; %)
S. noctilio	9,927	56,568	2,276 (4.02%)	1. France (1,398) 2. Spain (407) 3. Denmark (133)	1. Bosnia & Herzegovina (4.86%) 2. Denmark (4.81%) 3. Switzerland (4.84%)
L. invasa	8,536	120,258	967 (0.80%)	1. Brazil (749) 2. Spain (87) 3. Portugal (71)	1. Pakistan (0.96%) 2. Portugal (0.88%) 3. Argentina (0.88%)
O. maskelli	5,140	27,193	215 (0.79%)	1. Spain (81) 2. Portugal (77) 3. Brazil (27)	1. Burundi (1.01%) 2. Portugal (0.95%) 3. India (0.94%)

grained data are absent in most other regions – constraining scientists' ability to assess actual impacts (Bernal et al. 2018; Bukoski et al. 2022). Indeed, pests and their enemies exert impacts out of proportion with their individual biomass (Schmitz & Leroux 2020). For instance, single species of parasitic wasps often reduce pest infestation levels by 90% or even higher (Table 2). As such, ignoring their impacts in carbon models (Curtis et al. 2018) and flux maps (Harris et al. 2021) will cause errors and uncertainties. Those may explain the discrepancies in (tree-based) carbon sink size between studies (Harris et al. 2021). Our approach constitutes a first attempt towards addressing this omission.

In monoculture plantations, monophagous pests are prone to affect large portions of the canopy while feeding damage cannot be allayed through non-host tree growth compensation (Gansner et al. 1993; Anderson-Teixeira et al. 2021). As a result, invasive pests thrive in these settings (Nunez-Mir et al. 2017) and their carbon impacts surpass those in more diverse forest settings. Spread prevention through quarantine measures, a conservation of resident biological control agents or a targeted (or even pre-emptive; Avila et al. 2023; Hoddle 2024) introduction of effective, host-specific agents has benefits that require investigation. Across the developed and developing world, the active prevention of tree pests has only proven partially successful (Wingfield et al. 2015) and is hampered by complex, dynamic invasion patterns (Slippers et al. 2015; Garnas et al. 2016; Hurley et al. 2016). Our niche modeling reveals how each pest can find suitable areas beyond its current range. For instance, while *S. noctilio* is already established in many areas, it may still pose a threat to certain areas of North America, the Himalaya and Ural mountain ranges, Western Australia, Patagonia or Japan. Except for eastern North America and Argentinian Patagonia, these projections correspond with actual outbreak observations and earlier modeling results (Ireland et al. 2018). Its arrival in those settings carries immediate societal implications: new incursions and actual establishment of *S. noctilio* into Chile could inflict annual losses of US$ 18–76 per hectare and reduce economic returns of the national forestry sector by 2% (Allard et al. 2003). Our niche modeling approach should help to avert those socio-economic impacts by providing clear pointers on where to invest limited budgetary resources for pest prevention (e.g., Douma et al. 2017).

Reliable, fine-grained geographical distribution or spread maps are key to properly target investments in pest prevention and control. For *O. maskelli* and *L. invasa*, no climate niche modeling has previously been performed and our maps instantly inform biosecurity action including quarantine. While *L. invasa* occurs throughout most of its suitable areas (except for the eastern USA), *O. maskelli* is primarily confined to the Mediterranean basin and East African highlands. For the latter pest, quarantine measures are warranted in Andean nations, Mexico, Argentina, Brazil and southern China, and can help ensure future viability of eucalyptus wood farming in Iran (Eskandari et al. 2022).

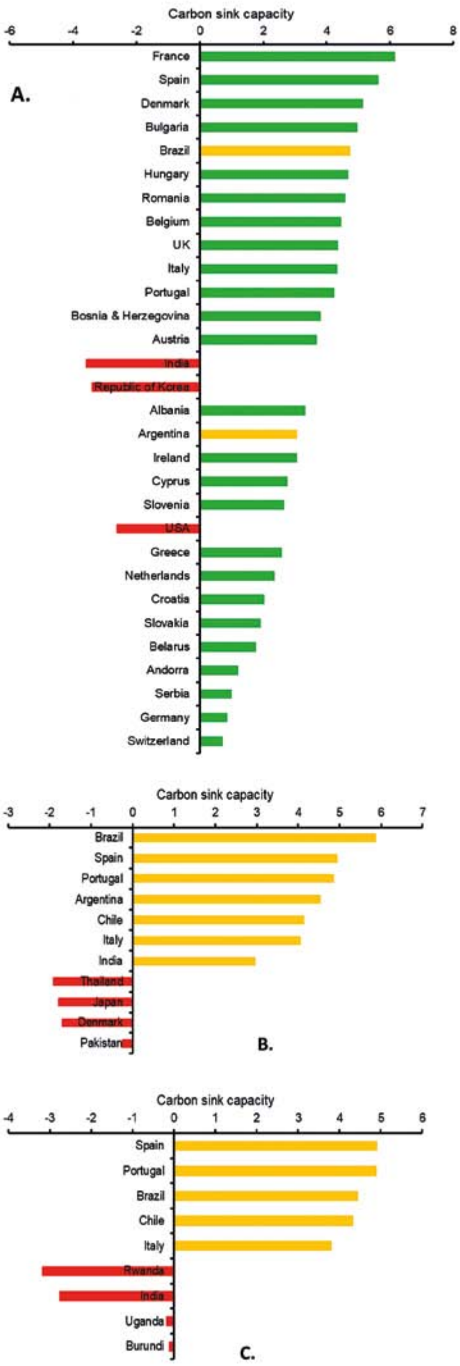

Fig. 2. Approximate conservation or restoration of the country-level carbon sink capacity for pest-afflicted tree plantations through biological control. Patterns are only plotted for *S. noctilio* (A), *L. invasa* (B) and *O. maskelli* in pine- or eucalyptus-growing countries for which digitized plantation extent data are available. Carbon sink capacity (tonnes of CO_2e yr^{-1}) values are log10(x+1) transformed. The extent of conservation (natural biological control) or restoration (classical biological control) of carbon sink capacity is shown in green or orange, respectively. Potential pest-induced loss of sink capacity is shown in red for countries where the pest remains unmitigated and/or experiences suitable climatic conditions. In the USA, natural enemies of native siricid wasps impact *S. noctilio* to varying extent, providing some level of natural biological control. Lack of plantation boundary data in other countries prevents an accounting of pest impact measures.

Our exercise thus guides preventative interventions to secure the socioeconomic, livelihood, and carbon sequestration role of tree plantations worldwide. Our distribution maps also carry value for a further delineation of invasion pathways, targeted deployment of novel monitoring and detection tools, and necessary phytosanitary measures e.g., on live plant movement or wood packaging material pathways (Slippers et al. 2015; Jactel et al. 2020; Quirion et al. 2021). To abate pest-induced losses in carbon sink capacity, multiple (non-exclusive) solutions are at hand. These comprise cultural, chemical, and biological control and breeding for host resistance (Hurley et al. 2016; Graziosi et al. 2020; Panzavolta et al. 2021). Given its human and environmental health hazards, monetary cost, intrinsic carbon footprint (Wyckhuys et al. 2022) and limitations by certification bodies such as FSC, chemical control is routinely discouraged in plantations. Instead, plantation managers favor low-carbon solutions including (natural, bred) resistance and amended management that effectively harnesses biodiversity and natural functionalities (Hartley 2002). In particular, biological control has proven to be a superb, sustainable solution for invasive pests (FAO 2011; Garnas et al. 2016; Wingfield et al. 2015; Kenis et al. 2019).

Biological control provides long-lasting, non-chemical control of all three focal pests in many invaded settings through an array of resident or (often accidentally) introduced mono- or oligophagous nematodes or parasitoids (Protasov et al. 2007; Fischbein & Corley 2015; Slippers et al. 2015; Kenis et al. 2019; Hajek & Morris 2021). Our modeling approach clearly illuminates its contribution to carbon sequestration and climate change mitigation. For *S. noctilio*, pest-related losses in carbon sink capacity are conceivably restored through natural biological control in its native range. In Spanish pine forests, for example, most *S. noctilio* are contained due to the combined action of resident parasitoids and nematodes (Lombardero et al. 2016). This top-down forcing however is often discounted and progressively degrading due to biodiversity loss and the precipitous decline in consumer organisms e.g., parasitoids or predators (Estes et al. 2011; Zhou et al. 2023). The same applies to parts of the *S. noctilio* invasive range where introduced natural enemies have proven effective, for example, in New Zealand and other parts of the southern hemisphere (Hurley et al. 2007; Slippers et al. 2015; Kenis et al. 2019). Similarly, classical biological control restored sink capacity in *L. invasa*- or *O. maskelli*-affected plantations across the Mediterranean (Mendel et al. 2017). Where this has not yet proven successful, new (molecular) technologies could help to revisit invasive pest issues (Hoddle et al. 2014). Aside from the scientifically-guided introduction of non-native natural enemies, other forms of biological control can also be consciously incorporated into plantation management. For instance, many plantation estates manufacture their own antagonistic or competitive microbiota such as *Trichoderma* spp. for pest or disease management (Flood et al. 2022). Similarly, kaolin dusting offers a non-pesticidal alternative where introduced natural enemies only provide partial control (Lo Verde et al. 2011). Hence, integrating biological control with other low-carbon measures as part of holistic plantation management offers a 'best-bet' approach to curb invasive pest impacts without inflicting further environmental damage (Jactel et al. 2021; Prospero et al. 2021).

Lastly, our study identifies several shortcomings in the current plantation extent dataset and the analytical approach that limit the accuracy and reliability of impact projections. These include 1) incomplete data for key pulp- or fiber-producing countries; 2) missing production figures for various tree species; 3) inability to differentiate between pest's region of origin and invasive range; 4) lack of data on inter- and intra-specific variability in tree susceptibility; 5) inability to account for mixed plantations and impact metrics tied to phenology; 6) incomplete understanding of environmental interaction or the extent to which tree death triggers increased growth of surrounding trees due to increased availability of light and water. Further, we recognize that our assumption of a linear relationship between pest damage and its climatic suitability – as per Flower & Gonzalez-Meler (2015) and Koontz (2021) – does not necessarily hold for all pests. For instance, *S. noctilio* experiences high climatic suitability and is readily established in eastern North America, though its impact is limited by the action of competing organisms, biological control agents and host tree resistance. Filling these knowledge gaps and resolving the other above-listed issues is imperative to ascertaining biotic impacts on carbon sequestration. It should prove fertile ground for future research. An upgraded plantation extent dataset complemented with well targeted ground-truthing e.g., tracking actual pest outbreaks instead of occurrences will be instrumental in generating more reliable, globe-encompassing projections.

Though exploratory in nature and constrained by data limitations, our work provides a first, global estimate of the extent to which biological control protects or reconstitutes carbon sink capacity in pests' native and invasive range. Given that the critical climate regulation service of tree systems is increasingly threatened by pest attack, the potential of biological control as a 'natural climate solution' requires urgent recognition. To secure the carbon fixation potential of planted trees, this practice is to become a frontline treatment in global forestry and plantation management.

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