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Gains and losses in ecosystem services and disservices after converting native forest to agricultural land on an oceanic island

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Highlights

- Ecological processes were assessed after converting Azorean forests to agriculture.
- All quantified ecosystem services/disservices showed idiosyncratic changes.
- Predation rates significantly decreased when forest was converted to cropland.
- Herbivory and pollination did not indicate significant changes.
- Decomposition and seed predation increased in high elevation maize fields and pastures.

Abstract

Habitat conversion to agricultural land is one of the main threats to terrestrial biodiversity and can affect ecosystem processes and cause changes in ecosystem services (ESs) and disservices (EDs). Yet, studies often rely only on the abundance and diversity of the service providers; the effects on ecological processes of habitat conversion are rarely directly monitored. In this study, we used the sentinel approach to evaluate how habitat conversion from native forest to agricultural land affected ESs and EDs on an oceanic island. We quantified herbivory on lettuce plants, invertebrate and vertebrate predation rates on artificial caterpillars, pollination on strawberry plants, seed predation on wheat and mustard seeds, and leaf decomposition rates in native forests, maize fields and pastures on Terceira Island, Azores (Portugal). Herbivory, invertebrate predation rates, and pollination service were not significantly different between habitats. Vertebrate predation rates in native forests (mean $6.1\% d^{-1}$) were significantly higher than that in pastures ($0.3\% d^{-1}$), or high-elevation maize fields ($0.5\% d^{-1}$), and marginally higher than in low-elevation

maize fields (2.2% d⁻¹). Overall seed predation after 48 h was significantly higher on wheat (mean 16.8%) than mustard seeds (5.6%). High-elevation maize fields also had higher seed predation (27.8%) than low-elevation ones (0.6%) or pastures (3.6%), but did not differ from the native forest (12.9%). Decomposition after 90 days was highest in pastures (78.4% and 45.9%, for tea and rooibos, respectively); although no significant differences between habitats were detected, except for low-elevation maize fields (64.4% and 33.6%). Conversion from native forest to cultivated land did not cause a clear decrease in the intensity of the studied ESs/EDs except for vertebrate predation. Using direct monitoring tools to simultaneously and consistently quantify multiple ecological processes is not only possible but needed, as ecological processes can respond differently to landscape changes.

Keywords: Azores, Ecosystem function, Environmental change, Habitat loss, Herbivory, Native forest, Pollination, Predation, Seed predation, Sentinel approach

Introduction

Humankind is a prevailing force of environmental change on Earth. In 2020, the mass of man-made objects (concrete, asphalt, glass, plastic, etc.) surpassed that of all living organisms (Elhacham *et al.*, 2020). Humans appropriate ca. 25% of the global net primary production (Andersen & Quinn, 2020), and human activities cause an estimated 1000-fold increase in the extinction rate of species (Vos *et al.*, 2015), threatening a drastic decrease in global biodiversity.

Although biodiversity has an intrinsic value and deserves moral consideration (Batavia & Nelson, 2017; Ives & Bekessy, 2015), the dominant attitude is that it is important because our survival depends on it (Cardinale *et al.*, 2012). Prominent drivers of the ongoing biodiversity loss are habitat conversion and fragmentation, overharvesting, pollution, climate change, and the spread of invasive species (Martins 1993; Young *et al.*, 2016), threatening the benefits humans derive from ecosystems (Leemans & de Groot, 2003).

For terrestrial ecosystems, the conversion of natural habitats to agricultural land is the primary threat (Martins 1993; Phillips *et al.*, 2017). An estimated 40% of the Earth's ice-free land has already been converted to cropland and pastures (Foley *et al.*, 2005; Ramankutty *et al.*, 2008). Habitat conversion to agricultural areas threatens the diversity and abundance of both invertebrates (Decaëns *et al.*, 2018; Klarner *et al.*, 2017; Larsen & Ormerod, 2010) and vertebrates (mammals: Bernard *et al.*, 2009; birds: Decaëns *et al.*, 2018, reptiles: Doherty *et al.*, 2020, amphibians: Greenberg *et al.*, 2018). Additionally, current agricultural practices often jeopardise ecosystem services (ESs) by negatively affecting ES providers.

The impact of agriculture on biodiversity is typically measured by assessing changes in the biotic community. Ecologists have a long tradition of tracking the abundance or presence of

species in a habitat (Henderson & Southwood, 2016), and these are frequently employed to characterise or track changes in ESs/EDs (e.g., Balzan *et al.*, 2014; Holland *et al.*, 2017). Yet, changes in the composition of ecological communities are not always reliable proxies when we are interested in function intensity (Rusch *et al.*, 2015). Therefore, a more consistent toolkit would be advantageous.

The sentinel approach holds promise to directly measure several ecological processes (e.g., herbivory, pollination, predation). Sentinels are exposed under field conditions to record natural processes and generate comparable quantitative data from different habitats. The main advantage of this approach is that it limits the effects of confounding factors because the characteristics of the sentinels, their densities, and distribution are decided *a priori*.

In this study, we used the sentinel approach to evaluate how habitat conversion from native forests to agricultural areas affected multiple ESs and EDs on an oceanic island. Oceanic islands hold a disproportionate share of global biodiversity, with many endemic species (Kier *et al.*, 2009; Warren *et al.*, 2015; Whittaker *et al.*, 2017), but individual islands may have depauperate biodiversity. Islands settled by humans have usually been profoundly modified (Whittaker *et al.*, 2017). Whether human colonisation and conversion to agriculture have decreased or increased ESs and EDs on islands is unknown. We quantified levels of herbivory, invertebrate and vertebrate predation, pollination, seed predation, and decomposition in native forests and two widespread cultivated habitats on Terceira Island of the Azores archipelago. The original landscape of Terceira was possibly modified by Viking sailors in the 9th-11th centuries and then by Portuguese colonisers in the 15th century (Gabriel *et al.*, 2015), but intensive agriculture associated with cattle farming (maize fields and pastures) began around 1960. We predicted that all the recorded ecological

processes will be affected by habitat conversion and that both ESs and EDs will be higher in cultivated landscapes because of their greater primary productivity.

Materials and methods

Study sites

This study took place on Terceira Island ($38^{\circ}37$ N- $38^{\circ}48$ N, $27^{\circ}02$ W- $27^{\circ}23$ W), the third largest (ca. 400 km²) and the second most populated island of the Azorean archipelago (Portugal) located in the North Atlantic Ocean. The climate of Terceira Island is oceanic, characterised by cool summers and winters, but the southern part at low altitudes has hot and dry summers (average maximum air temperature between 24- 26° C. Couto, 2011). The annual precipitation ranges between 750 and 3000 mm, with higher levels in winter and at higher altitudes. Originally, the island was mostly forested but today <5% remains (Elias *et al.*, 2016). The main agricultural habitats are semi-natural pastures, intensive pastures and maize fields (in rotation with intensive pastures in the summer), which are extensively grown on the island since the 1960s. Orchards and vineyards are also present and were planted by the Portuguese colonisers of the archipelago in the 15th century.

We assessed the level of five ecosystem processes (herbivory, predation, pollination, seed predation, and decomposition) leading to ESs and EDs in four habitats: the native forests, pastures (intensive) at high altitude, and low- and high-elevation maize fields (Figs. 1 and 2). Low- and high-elevation maize fields were considered different habitats because, although the same crop being planted at ca. 200 m difference in altitude, they have a different phenology and rotation cycle. Low-elevation maize fields are sown and harvested about one to two months earlier than

high-elevation fields, and are grown in annual rotation with pastures, while high-elevation maize fields are grown in 3- to 5-year rotations with pastures. The four habitats were at least 6 km distant from Angra do Heroísmo, the largest urban centre of Terceira. No significant landscapes changes in our study sites occurred in the previous 20 years.

The native forest sites were located at 430-630 m above sea level (asl) and included protected areas where human activities are restricted. The main vegetation in these sites consisted of trees and shrubs including Laurus azorica, Juniperus brevifolia, Ilex azorica and Erica azorica. The three agroecosystems were surrounded by comparable landscapes composed of patches of cultivated areas and small villages and farm buildings but differed in their elevation. Lowelevation maize fields were located at 50-170 m asl, were grown between April and September, and were at least 5 km away from the native forests. High-elevation maize fields and intensive pastures were located at 275-315 m asl, grew between May and October (maize) and were located at least 2.5 km from the native forests. Intensive pastures at high elevations consisted of a mixture of perennial ryegrass (Lolium perenne) and white clover (Trifolium repens). All cultivated study sites were conventionally managed with regular applications of fertilizers, pesticides, and herbicides, particularly at the beginning of the maize cropping season. Intensive high-elevation pastures were also subjected to high grazing pressure. Each habitat was represented by three sites at least 300 m from each other. High-elevation study sites were either in the first or second year of the crop rotation cycle. The assessments were performed between the end of June and late September 2020, corresponding to ca. one week before maize flowering and kernel ripening, respectively. Low- and high-elevation maize fields were sampled at the same phenological stages and pastures were sampled during flowering.

Assessing herbivory

We quantified herbivory by exposing sentinel lettuce (*Lactuca sativa* cv. White Boston, RJS Sementes, Portugal) plants grown in 5 L pots in the greenhouse at the University of the Azores, Angra do Heroísmo campus. In each site, six plants were exposed for two weeks. Overall, we assessed 18 plants each in native forests, low- and high-elevation maize fields and 14 plants in the pastures. Four plants exposed in pastures were excluded from the analysis since they were destroyed by cows. Herbivory rates were visually estimated as in Ferrante *et al.* (2022).

Assessing predation

We quantified predation rates using the artificial caterpillar method (Howe *et al.*, 2009). Green plasticine caterpillars (Smeedi plus, V. nr. 776609, Denmark) 15 mm long and 3 mm in diameter were exposed on the ground along two 50 m transects at every 2 m. After 48 h, caterpillars were checked for signs of attack (Low *et al.*, 2014). Between early July and early September 2020, two assessments were performed in each habitat using 150 caterpillars on each occasion and habitat. Thirty-two caterpillars were lost (2.7%; 10 in the native forests, 10 and 6 in low- and high-elevation maize fields, respectively, and 4 in pastures) and were excluded from the analysis.

Assessing pollination

We assessed pollination using strawberry plants (*Fragaria x ananassa* cv. San Andreas). Plants were grown in a greenhouse and were brought to the field when they had five flowers. Excess buds were manually removed. Plants were exposed for two weeks and pollination service was estimated by calculating the seed set per fruit as in Ferrante *et al.* (2022). Aborted or damaged buds (n = 112, 31.1%) were considered lost and were excluded from the analysis. One plant exposed in a pasture was excluded because all five of its buds were damaged.

Assessing seed predation

Seed predation was quantified using modified seed boxes of two types: one allowed access to all seed predators and the other excluded vertebrates, as in Ferrante *et al.* (2022). Predation of mustard (*Sinapis alba*) and wheat (*Triticum aestivum*) seeds were considered an ES and ED, respectively, as mustard is often a weed in arable land (Didon & Boström, 2003). After 48 h, boxes were collected and missing or damaged seeds were considered predated. Sampling was repeated twice between July-September 2020, using 12 seed boxes per site, for a total of 288 seed boxes throughout the experiment. Three seed boxes were found displaced at the time of collection and were removed from the analysis.

Assessing decomposition

We quantified decomposition of organic material using the tea bag method (Keuskamp *et al.*, 2013). Pairs of tea and rooibos bags were exposed for 90 days under field conditions at 10 cm depth in the soil. After this time, bags were collected and dried at 55° C for a minimum of 48 h. Before and after the field operations, the organic and synthetic portions (bag, string, and label) of the bags were weighed (KERN MRS 120-3 balance, sensitivity 0.001 g). At each site, five pairs were exposed at ~15 m from each other. The loss of organic material was calculated as the difference between the original mass and the average mass of the synthetic portion (mean = 0.2518 g, SD = 0.003 g, n = 10) and the remaining tea/rooibos mass. Because of farming activities, several bags (n = 58, 48.3%) in low- and high-elevation maize fields and pastures were destroyed or damaged and were excluded from the analyses.

Statistical analyses

All statistical analyses were carried out using the R software (R Core Team, 2021) through RStudio (RStudio Team, 2021) and the R packages *performance* (Lüdecke *et al.*, 2021), *ggeffects* (Lüdecke, 2018), and *lsmeans* (Lenth, 2016). All linear models met the parametric assumptions.

Herbivory rates in the four habitats were compared using a linear mixed model (LMM) where herbivory damage on a leaf (%) was the response, the habitat was considered as a fixed factor, and the plant ID and the site were included as random factors.

Predation rates were analysed using generalised linear models (GLMMs) with a binomial distribution and logit link function, where the habitat was the fixed factor and the site as a random factor. This model was tested on three responses: overall, vertebrate, and invertebrate predation rates. Partitioning predation rates is better than pooling all predators, as the same factors may have opposite effects on vertebrate and invertebrate predators (Ferrante *et al.*, 2017).

We calculated the ratio between the average number of seeds per fruit for every pair of pollinator-accessible and pollinator-inaccessible plants (hereafter "seed set ratio"). A seed set ratio ≤ 1 indicates that insect pollination was negligible. Pollination was analysed using an LMM where the seed set ratio was the response, the habitat was considered as a fixed factor, and the plant ID and the site were random factors.

Seed predation was analysed using an LMM where the log-transformed seed predation rate (%) was the response and the habitat (native forest, pastures, maize fields), the seed species (mustard vs. wheat) and the box type (open vs. vertebrate-inaccessible) were considered fixed factors, and the box ID and site were random factors. Moreover, as seed predation occurs patchily, we tested the probability that at least one seed in a seed box was predated using a GLMM with a binomial distribution and logit link functions where seed box predation was the (binary) response,

the habitat, the seed species, and the box type were fixed factors, and the box ID and the site random factors.

Decomposition was analysed using an LMM where organic mass loss was the response, habitat, and bag type (tea vs. rooibos) were fixed factors, and site was a random factor.

Results

Herbivory

The average leaf damage on a lettuce plant after two weeks was 19.5% (SE = 3.7%, n = 68). The highest herbivory rates were found in high-elevation maize fields (mean = 52.9%, SE = 10.2%, n = 18 plants), including one site where all six lettuce plants were entirely consumed by noctuid caterpillars. This was followed by the native forests (mean = 13.9%, SE = 2.6%, n = 18), low-elevation maize fields (mean = 4.9%, SE = 1.3%, n = 18), and pastures (mean = 2.5%, SE = 0.9%, n = 14). No significant differences were detected between these habitats (Fig. 3). The largest variability between sites was found in high-elevation maize fields (SE = 2.9%, n = 3), followed by native forests (SE = 1.7%, n = 3), pastures (SE = 1.4%, n = 3), and low-elevation maize fields (SE = 0.6%, n = 3).

Predation

Eighty-eight caterpillars showed attack marks after 48 h (7.5%, n = 1168). Invertebrates accounted for 39.8% of the attacks, followed by rodents (35.2%), and birds (23.9%). Invertebrate attacks were recorded in all habitats but mainly in high-elevation maize fields (40.0% of all invertebrate attacks), followed by pastures (28.6%), native forests (17.1%), and low-elevation

maize fields (14.3%). Most rodent attacks were detected in the native forests (90.3% of all rodent attacks) and in high-elevation maize fields (9.7%), while no rodent attack mark was observed in low-elevation maize fields or pastures. Bird attacks were most frequent in low-elevation maize fields (61.9% of all bird attacks), followed by the native forests (28.6%), and pastures (9.5%), while no bird attacked the caterpillars exposed in high-elevation maize fields.

The highest overall predation rates were recorded in the native forests (mean = 7.1% d⁻¹, SD = 1.8% d⁻¹, n = 3 sites), followed by low- (mean =3.1% d⁻¹, SD = 2.3% d⁻¹, n = 3) and high-elevation maize fields (mean = 2.9% d⁻¹, SD = 2.1% d⁻¹, n = 3), and pastures (mean = 2.0% d⁻¹, SD = 0.5% d⁻¹, n = 3).

The overall predation rates in the native forest were significantly higher than in any other habitat (p < 0.001 - 0.038), but no other difference in overall predation rates was detected between other habitats. There were no significant differences in invertebrate predation rates between habitats, while vertebrate predation rates in the native forests (mean = 6.1% d⁻¹, SD = 2.0% d⁻¹, n = 3) were significantly higher than that in pastures (mean = 0.3% d⁻¹, SD = 0.3% d⁻¹, n = 3; p = 0.001), high-elevation maize fields (mean = 0.5% d⁻¹, SD = 0.9% d⁻¹, n = 3; p = 0.001), and marginally higher than in low-elevation maize fields (mean = 2.2% d⁻¹, SD = 2.2% d⁻¹, n = 3; p = 0.065, Fig. 3).

Pollination

The highest seed set ratios were found in pastures (mean = 1.28, SD = 0.61, n = 8) and native forests (mean =1.28, SD = 0.50, n = 9). The seed set ratios in high-elevation maize fields (mean = 1.02, SD = 0.42, n = 9) and low-elevation maize fields (mean = 0.88, SD = 0.42, n = 9) were \leq 1, suggesting that no insect pollination occurred. No significant differences were detected

between the seed set ratios in the four habitats (Fig. 3). The largest variability between sites was found in high-elevation maize fields (SD = 0.29, n = 3), followed by native forests (SD = 0.25, n = 3), low-elevation maize fields (SD = 0.14, n = 3), and pastures (SD = 0.11, n = 3).

Seed predation

More than half of the seed boxes (52.6%, n = 150) showed no sign of predation. Two open wheat seed boxes and two vertebrate-exclusion wheat seed boxes were completely emptied (100% predation) in both high-elevation maize fields and in native forests. The probability that at least one seed in a box was predated was higher for wheat grains than mustard seeds (p = 0.001, GLMM), while no difference was detected between open and vertebrate-exclusion boxes (p = 0.245, GLMM). In addition, more seed boxes showed predation events in high-elevation maize fields (mean = 0.78%, SD = 0.42%, n = 72) than in any other habitat (p < 0.001 - 0.017). Seeds were less predated in low-elevation maize fields (mean = 0.15%, SD = 0.36%, n = 71) than in native forests (mean = 0.50%, SD = 0.50%, n = 70; p = 0.001), or pastures (mean = 0.46%, SD = 0.50%, n = 72; p = 0.005), while the probability that at least one seed in a box was predated did not differ between native forests and pastures (p = 0.965).

Similarly, seed predation was significantly higher on wheat (mean = 16.8%, SD = 30.0%, n = 143; Table 1) than mustard seeds (mean = 5.6%, SD = 13.8%, n = 142; p < 0.001, LMM), but not significantly different between open (mean = 12.5%, SD = 24.4%, n = 142) and vertebrate-exclusion seed boxes (mean = 10.0%, SD = 23.6%, n = 143; p = 0.172, LMM), and was significantly higher in high-elevation maize fields (mean = 27.8%, SD = 32.4%, n = 72) than pastures (mean = 3.6%, SD = 6.7%, n = 72; p < 0.001, lsmeans) or low-elevation maize fields (mean = 0.6%, SD = 1.8%, n = 71; p = 0.012, lsmeans), but not significantly higher than in the native forests (mean = 12.9%, SD = 27.9%, n = 70; p = 0.145, lsmeans; Fig. 3). The largest

variability between sites was found in high-elevation maize fields (SD = 21.2%, n = 3), followed by native forests (SD = 8.0%, n = 3), pastures (SD = 1.8%, n = 3), and low-elevation maize fields (SD = 0.2%, n = 3).

Decomposition

After 90 days exposure, tea and rooibos bags lost on average 71.8% and 38.9% of their original mass, respectively. The highest loss was registered in pastures and high-elevation maize fields, followed by native forests and low-elevation maize fields (Table 2). Mass loss was significantly higher (p < 0.001, LMM) on tea than on rooibos and in pastures than low-elevation maize fields (p = 0.0341, lsmeans), while no significant differences were detected between other habitats (Fig. 3).

Discussion

We found that the native forest always had intermediate levels of ESs/EDs, except for predation. None of the quantified ESs/EDs was consistently the highest or lowest in any habitat. No significant differences were detected in herbivory, invertebrate predation, and pollination. Vertebrate predation was significantly higher in the native forest than in low- and high-elevation maize fields and pastures, mostly because of the contribution of non-native rodents. Seed predation was significantly higher in high-elevation maize fields than in low-elevation maize fields and pastures. Decomposition was significantly higher in pastures than in low-elevation maize fields. These data contribute to filling a knowledge gap because there is a general lack of quantification and comparison of ecological processes between different habitats from islands (reviewed by Sieber *et al.*, 2018).

Our results highlight how complex the effects of habitat transformation on ecosystems can be, as ESs and EDs were not unequivocally higher or lower than the baseline levels obtained from the natural habitat (the Azorean native forest). This was in contrast to our hypothesis that these ecological processes were more intense in agricultural habitats because of their higher productivity and the presence of non-native species more closely associated with cultivated habitats. Thus, our results suggest that biomass productivity itself, which is typically higher in agricultural habitats, may be a poor predictor for the levels of ESs/EDs.

Interestingly, the levels of several ecological processes were similar in native and agricultural habitats, suggesting that non-native species, which abound in the latter, can functionally replace native species and even add new functions (Rigal et al., 2018). In Hawaii, for example, non-native pollinators accounted for more than 72% of the visits to 15 native plant species, five of which are not visited by native pollinators (Shay et al., 2016). Although our methodology did not allow us to precisely identify ES and ED providers, non-native species likely played an important role in both ESs and EDs. On Terceira, non-native species dominate the arthropod communities in low- and high-elevation maize fields (Borges et al., 2021) as well as intensive pastures (Florencio et al., 2015), although some endemic generalist species and some native non-endemic species are also adapted to agroecosystems. Similarly, non-native species are important members of the arthropod communities in native Azorean forests (Brush et al., 2022) and are increasing in diversity (Borges et al., 2020). Anthropogenic habitats and their associated non-native species usually increase local species richness and expand the originally existing functional space on oceanic islands (Rigal et al., 2018; Whittaker et al., 2014), generating ecological opportunities (Rigal et al., 2018). Agricultural habitats host many non-native species on Terceira Island (Rigal et al., 2018), which can explain the relatively similar levels of ecological

processes in agricultural habitats and the native forests. Non-native species, despite their threat to native communities on islands (Borges *et al.*, 2019, 2020), also provide provisioning, regulating and cultural ESs (Pejchar & Mooney, 2009), sometimes of higher economic value than native species (Riley *et al.*, 2018).

Herbivory was not significantly different between habitats. This was a consequence of the great variability among sites, which indicated that this ecological process occurred patchily, even reaching infestation levels, as observed in high-elevation maize fields. Herbivory rates in high-and low-elevation maize fields and native forests were higher than those recorded in Azorean vineyards or orchards (Ferrante *et al.*, 2022), possibly because these habitats host more herbivores than vineyards or orchards do (Borges *et al.*, 2021).

Predation rates were significantly higher in the native forests than in pastures or maize fields, but this difference was due to the contribution of non-native rodents that showed higher activity in the native habitat. Previous studies indicated that black rats (*Rattus rattus*) forage in the Azorean native forests to prey upon vertebrates (e.g., Lamelas-López *et al.*, 2021) and plants (Ceia *et al.*, 2017). Since rodents were the main predators in our study, a direct benefit from the proximity of native forests to the agroecosystems is unlikely. Invertebrate predator attacks were not significantly different between habitats and were comparable to levels found in other habitats on Terceira (Ferrante *et al.*, 2022), but lower than in continental agroecosystems (González *et al.*, 2014).

The levels of pollination recorded confirmed that pollinator activity on Terceira Island was high in native forests but also in intensive pastures. Maize fields, even though pollinators collect pollen also from wind-pollinated plants like maize (Saunders, 2022), had a notably lower pollination activity. Arable land-dominated landscapes do not necessarily have reduced pollination

levels, and can support high pollinator activity, at least in mainland Europe (Herbertsson *et al.*, 2021). Picanço *et al.* (2017a) found that the bee communities are both abundant and diverse in the Azorean native forests and semi-natural pastures (characterised by *Lotus* sp., *Holcus* sp., *Rumex* sp. and other herbs). Interestingly, the intensity of the pollination service in native forests and pastures was comparable, although provided by different species (Picanço *et al.*, 2017b). This underlines the importance of using direct quantification of ecological processes instead of basing ES estimations only on the presence or relative abundance of ecosystem service providers.

Higher seed predation rates were found in high-elevation maize fields and native forests than elsewhere. Because of the high humidity, native forests host numerous invertebrate species, including seed predators such as slugs (Miczajka *et al.*, 2019; Türke *et al.*, 2010). The seed predation rates in these habitats were much higher than in vineyards and orchards on Terceira Island in spring and early summer (Ferrante *et al.*, 2022), but similar to those recorded in late summer (unpublished results), which suggests that seed predators with activity peaks in summer, such as ground beetles (Borges, 1995; Borges & Serrano, 1993) could have been responsible.

The decomposition rates were also higher than those in vineyards and orchards (Ferrante *et al.* 2022), and about twice as high as those recorded on mainland Europe (Houben *et al.*, 2018). This could be related to the mild to warm temperatures and uneven but abundant precipitation that characterises the oceanic climate of Terceira. Low-elevation maize fields receive less precipitation and experience higher temperatures (Azevedo *et al.*, 1999; Elias *et al.*, 2016), leading to lower microbiological activity (Kakumanu *et al.*, 2019; Lopes *et al.*, 2021), and slower decomposition.

Most of the quantified ecological processes ran at lower intensity on Terceira Island than on the European mainland. Oceanic island communities are disharmonic, typically harbouring only a subset of the species pool present on the mainland, not only with lower species richness but fewer

functional groups (Whittaker & Fernández-Palacios, 2007). This pattern emerges due to a dispersal barrier, but colonising species need also to overcome the biotic resistance by the local community although facilitation processes can also occur (Olesen *et al.*, 2002).

In this study, we focused on five ecological processes that are at the basis of sustainable agricultural and ecosystem functioning, but we did not include other essential ESs provided by forests, such as climate regulation, clean air and water, soil erosion mitigation, recreation, and wildlife habitat (Förster *et al.*, 2021; Smail & Lewis, 2009). Several of these services cannot be easily replaced and habitat conversion to agricultural land will inevitably mean their loss and that of several native or endemic species.

The complex interaction between human societies and local-regional environmental conditions (Norder *et al.*, 2020) is particularly relevant on islands since they hold a disproportionately large share of global biodiversity (Kier *et al.*, 2009; Warren *et al.*, 2015; Whittaker *et al.*, 2017) and the current biodiversity crisis disproportionately impacts them (Borges *et al.*, 2019). The extent to which biodiversity loss will affect ES provisioning is difficult to quantify but it is likely to be enormous. Despite the continued use of abundance and species trait proxies to assess ES levels (Noriega *et al.*, 2018), the limits of such an approach have been recognised (Balvanera *et al.*, 2022). Standardised data on multiple ESs and EDs, as we have done here, will provide decision-makers with additional information to more appropriately manage the natural capital.

Conclusions

Despite intense research on ESs in the last decades, few studies utilise a multi-ecosystem services approach (Nieto-Romero *et al.*, 2014; Seppelt *et al.*, 2011; Wang *et al.*, 2015), such as the one used in the current study, and EDs are rarely measured. This study shows how several monitoring tools based on the sentinel approach can be simultaneously used to directly monitor the effects of land-use change on ESs and EDs. These methods can usefully complement the more widely used "structural proxy" approach, based on service/disservice providers. Land-use change and landscape simplification are persistent threats to biodiversity and ESs worldwide, and vigorous conservation efforts are needed if we want to achieve the global biodiversity-saving targets (Tittensor *et al.*, 2014). In light of the several environmental changes that characterise the Anthropocene, future work will need to seek agricultural practices that are not only resilient, and sustainable over the long term but also compatible with biodiversity and ESs conservation (Tilman *et al.*, 2002).

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Declaration of Competing Interest

The authors declare that they have no competing financial interests.

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Table 1. Mean seed predation (\pm SE) of wheat and mustard seed in open and vertebrateexclusion seed boxes in the Azorean native forest, pastures, and high- and low-elevation maize fields. Sample size is 18 for all combinations except for those marked with an asterisk, which had n = 17.

	Seed predation (% after 48 h)				
Habitat	Wheat			Mustard	
	Open	Exclusion	Open	Exclusion	
Native forest	22.6 (8.4)*	25.2 (9.1)	2.1 (1.2)*	1.4 (0.8)	
Pasture	7.4 (2.4)	2.2 (0.8)	3.3 (1.5)	1.6 (0.8)	
Maize, high	42.6 (8.6)	33.1 (9.1)	19.8 (6.1)	15.7 (4.6)	
Maize, low	1.6 (0.7)	0	0.2 (0.2)	0.6 (0.4)*	

Table 2. Mean decomposition (mass loss/original mass \pm SE) of tea and rooibos bags in the Azorean native forest, pastures, and high- and low-elevation maize fields. Sample size is 15 for all combinations except for those marked with an asterisk, which had n = 14.

	Decomposition (g after 90 days)		
Habitat	Tea	Rooibos	
Native forest	69.5 ± 1.3	37.3 ± 1.2	
Pasture	$78.4 \pm 1.2*$	45.9 ± 1.4	
Maize, high	80.0 ± 0.8	$43.4 \pm 1.2*$	
Maize, low	64.4 ± 1.2	33.6 ± 1.6	

Figures

Fig. 1

Fig. 1. Map of Terceira Island and its main habitats. Adapted from Borges et. al, 2022.

Fig. 2

Fig. 2. Native forests (A), low-elevation maize fields (B), high-elevation maize fields (C), and pastures (D) on Terceira Island, Azores.

Fig. 3

Fig. 3. Levels of the intensity of herbivory, overall predation, invertebrate predation, vertebrate predation, pollination, seed predation and decomposition in the Azorean native forests, low- and high-elevation maize fields, and pastures. Different letters indicate significant differences among habitats and ecological processes (p < 0.05).





Fig. 2



John







_graphical abstract