

Quantifying the ecosystem service of scavenging by the sentinel method

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QUANTIFYING THE ECOSYSTEM SERVICE OF SCAVENGING BY THE SENTINEL METHOD

LAVIGNE LAMBERT

**TRAVAIL DE FIN D'ETUDES PRESENTE EN VUE DE L'OBTENTION DU DIPLOME DE
MASTER BIOINGENIEUR EN SCIENCES AGRONOMIQUES**

ANNÉE ACADÉMIQUE 2020-2021

(CO)-PROMOTEUR(S): FRANCIS FRÉDÉRIC; LÖVEI GABOR

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This experimentation took place in the archipelago of the Azores, in Terceira (Portugal) at the University of the Azores in the Department of Environmental Sciences, and in Denmark at the Flakkebjerg Research Centre in the Department of agroecology of the University of Aarhus.

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Abstract

Scavenging as an ecosystem service is largely understudied. In this work, we aimed to measure scavenging levels in different habitat types on the Macaronesia Island of Terceira, Portugal, and on the island of Zealand, Denmark. The habitats studied in Terceira were orchards, vineyards, native forest, and urban areas. In Denmark the habitats were fields (wheat), edge fields, primary forest, and urban areas. We used fly larvae glued to cardboard squares to measure scavenging rates. The boxes were exposed during the day and night and checked every 2 hours to monitor changes in scavenging levels. The overall levels of scavenging were 64.5% in Terceira and 29.5% in Denmark by arthropods. These levels were much higher than expected.

Le charognage en tant que service écosystémique est largement sous-étudié. Dans ce travail, nous avons cherché à mesurer les niveaux de charognage dans différents types d'habitats sur l'île Macaronésienne de Terceira, au Portugal, et sur l'île de Zealand, au Danemark. Les habitats étudiés à Terceira étaient des vergers, des vignobles, la forêt native et des zones urbaines. Au Danemark, les habitats étaient des champs (blé), des bordures de champs, la forêt primaire et des zones urbaines. Nous avons utilisé des larves de mouches collées sur des carrés de carton pour mesurer les taux de charognages. Les cartons ont été exposés pendant le jour et la nuit et vérifiés toutes les 2 heures pour suivre les changements dans les niveaux de charognage. Les niveaux globaux de charognage, étaient de 64.5% à Terceira et de 29.5% au Danemark par les arthropodes. Ces niveaux étaient beaucoup plus élevés que prévu.

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Introduction

The impact of agriculture on ecosystems

Between 11,000 and 9,000 years ago, the first human civilisations domesticated plants and developed agriculture. Over time, agricultural methods were perfected, resulting in generally higher yields. However, the main changes took place after the Second World War, as modern agriculture was established during this period. Indeed, war mechanisation and chemical technologies were relocated in agriculture to increase yields (Dimitri et al., 2005). When research to optimise agriculture began, mechanical and chemical warfare technologies were relocated to agriculture to increase yields (Jones et al., 2017). The aim was to optimise production systems to move towards more intensive agriculture. The idea is to achieve optimal production, i.e., to have the best possible yields while minimising production costs. Today, intensive agriculture is the main agricultural production system in the world. Developing countries having benefitted from the “green revolution” starting in the 1960ies. The green revolution is a mix of political actions, scientific breakthroughs, and intensive agricultural mechanisation. The purpose was to address the demographic growth and ensure food security. The paradigm shift allowed significant yield increases, with chemical inputs, monocultures, and the development of modern grain cultivars. In 40-50 years, fertiliser use has risen by 500% and irrigation doubled, which has contributed to environmental pollution, degraded water quality and increased pressure on water resources while consuming more fossil energy (Foley et al., 2005, 2011). The results of this pattern shift are deeply rooted in the ecosystems.

Today, agricultural land, either grassland or cropland, represents almost 40% of the global ice-free land area and is the largest biome on earth (Foley et al., 2005). Agricultural land is divided as follows: 62% is used for crops that feed people, 35% for animal husbandry and 3% for biodiesel production (Foley et al., 2011). However, arable land is limited, as for the most common crops, between 1985 and 2005, their cultivated area increased by 2.4% while their yield increased by 30% (Foley et al., 2011). Genetic progress has compensated for the lack of arable land. Nevertheless, since 1996, crop yields have stagnated in Europe, especially for hard wheat, due to climate change¹. Thus, to meet the growing demand for consumer goods, more and more natural ecosystems are being replaced by agricultural land and intensively managed by agribusiness companies. These practices have significant

environmental costs, the expansion (replacement of ecosystems by agricultural land) is responsible for 27% of global deforestation between 2001 and 2015, in Indonesia over the same period, it is 20% of the national forest that has been converted by palm oil plantations or grasslands. (Austin et al., 2019; Curtis et al., 2018). Moreover, deforestation releases a large amount of dioxide carbon in the atmosphere and contributes to climate change. Today, agriculture is the 3rd largest greenhouse gas emitting sector after the industry and the energy sectors (Keramidas et al., 2018). Intensive agricultural practices such as monoculture and ploughing lead to a loss of habitats and biodiversity and contribute to soil degradation. This involves a loss of ecosystem services linked to life in soils such as carbon storage or the destruction of mycelial networks that are beneficial for soil structure and crops (Gosling et al., 2006). Overall, these practices prevent maintaining a high level of biodiversity (El Chami et al., 2020), indeed, the expansion and intensification of agricultural land are the two of the most damaging factors for the environment (Foley et al., 2011). This is a big concern because ecosystem services depend on biodiversity (Bennett et al., 2015; El Chami et al., 2020; Isbell et al., 2017). Intensive agriculture is not resilient, this is the reason why climate change deeply affects modern farming. The consequences are that we are exposing ourselves to even more radical changes (El Chami et al., 2020).

Although agricultural progress has reduced food insecurity around the world, there are still several densely populated regions where food security is not ensured, nor is it seen to be happening soon. According to the FAO (Food and Agricultural Organization) between March and July 2021, 20 countries have experienced or will experience a deterioration in their food security. The causes are multiple and interdependent: war, unstable political situation, COVID19, economic shock, crop pests and diseases, climate change, etc. These consequences are the evidence that the whole agriculture system is unsuitable to cope with the challenges of the future. Indeed, climate change will increase inequalities in terms of available resources, especially water. Tensions between countries over this resource will be exacerbated by issues of national sovereignty (Strzepek & Boehlert, 2010). It is therefore important to develop a more sustainable, resilient, ethical, and socially sensitive agriculture to meet the challenges of climate change (Foley et al., 2011; Garnett et al., 2013; Ghosh et al., 2020). Thus, one solution could be to focus agriculture with lower environmental damage.

Climate change and the challenges for agriculture

Climate change and agriculture are strongly connected. Agriculture is responsible for a significant share of the increase in greenhouse gases and therefore actively contributes to climate change (Malhi et al., 2021; Raza et al., 2019). Global warming is the main threat to agricultural production and food security by increasing biotic and abiotic pressures (Raza et al., 2019). In summary, agricultural yields can be expected to decrease, stresses related to annual precipitation variations, extreme heat and weather events, changes in pest/weed populations, loss of soil fertility, decreased metabolic activity of plants and sea level fluctuations (Malhi et al., 2021; Raza et al., 2019). Lastly, climate change is also expected to have socio-economic consequences by contributing to increased global inequalities. Ultimately, agriculture is the human activity most threatened by climate change (Raza et al., 2019).

It is therefore important to implement a new way of production to mitigate the negative impacts of conventional agriculture. Firstly, modifying food production by diversifying agroecosystems, increasing genetic diversity, and implementing crop mixtures could help to strengthen its resilience (Isbell et al., 2017). Similarly, improving the efficiency of use of agricultural resources such as fertilisers with the purpose to reduce yield gaps between different parts of the world is a critical aspect to consider (Foley et al., 2011). Therefore, adaptation strategies have been suggested to reduce both the environmental impact of agriculture and the impact of climate change on agriculture while considering a societal response. These strategies can be based on technologies that help to implement smart, crop-specific resource use practices considering environmental and weather conditions while reducing carbon emissions and other greenhouse gases such as methane and nitrous oxide (Malhi et al., 2021). Adaptation strategies can also be based on agricultural management practices where the objective is to take advantage of the interactions between plants and their biotic and abiotic environments (Power, 2010). IPMs (integrated pest management), for example, seek to give priority to natural regulatory processes while allowing for more conventional interventions once pest thresholds have been exceeded. ACPs (agroecology crop protection) focus more on maintaining biodiversity and soil health to make ecosystems more resilient to biotic stress (Deguine et al., 2021). The aim is to increase the overall health of ecosystems to increase the ecosystem services they can provide (Deguine et al., 2021; Power, 2010). Indeed, the more diverse an ecosystem is, the more resilient it is to climate

change disturbances (Perovic et al., 2015) and therefore the more ecosystem services it can maintain.

Finally, reduce food waste is another important aspect to reduce the ecological footprint of agriculture. Indeed, according to the estimations, all steps of the food production have a lot of losses, in total almost 25% are wasted each year (Kummu et al., 2012; Stancu et al., 2016). In other words, the occupancy of almost 30% of agricultural lands, the equivalent of 1.4 billion hectares or 3.3 billion tonnes of CO₂ release into the atmosphere per year happens for nothing (Paritosh et al., 2017). In addition, improving the food supply should help to decrease malnutrition across the world (Foley et al., 2011). Consumers have a responsibility, it is necessary to change our diet to limit negative impacts on the ecosystems (Foley et al., 2011).

Scavenging as an ecosystem service (ES)

Ecosystem services (ES) are an anthropogenic view of the relationship between nature (biotic and abiotic) and human activities. Consequently, although the concept of ES is not new in the scientific community, it is still complicated to define them globally (Danley & Widmark, 2016). However, debates on ES revolve around three interdependent and overlapping concepts: the physical structure of the ecosystem, the interaction of ecosystem components, and the contribution of the ecosystem to human well-being. (Danley & Widmark, 2016). Nevertheless, the most common notion of ES is that of a hybrid ecological and economic approach, which makes direct links between the functions and processes of nature and the benefits they generate (Danley & Widmark, 2016). Thus, it is understandable that through the debates they generate, ES have an ambivalent status both scientifically and politically. It is in this context that the European Commission has tried to define ES as :“the aspects of ecosystems utilised (actively or passively) to produce human wellbeing” (“Protecting Natural Capital for Human Wellbeing and Sustainable Development Evaluating Biodiversity and Ecosystem,” 2010). These services play a vital role in our lives. In January 2018, the International Classification of Ecosystem Services (CICES) published an update of the ES classification. Thus, the CICES counts more than 90 ESs divided into 6 sections. The 6 sections are: cultural biotic and abiotic, all the non-material, non-consumable inputs that ES provide via ecosystems. They directly affect the physical and mental states of people. Provisioning biotic and abiotic i.e., all nutritional, non-nutritional, material, and energy products of living organisms as well as abiotic inputs (including water). Regulation & Maintenance biotic and abiotic, all actions of organisms on the environment that may affect

human health, safety or comfort (Haines-Young & Potschin, 2018). The preservation, understanding and enhancement of ES is therefore very important. Indeed, there is a link between ES and human well-being, ES provide us the basic needs. The global worth of these ES is invaluable, and for the future it will be important to enhance ES through better management of the environment. Agriculture plays and will play an important role in the conservation of ES through the development of new means of production. In practice, the results are encouraging, for example, the association crops (different varieties of cereals) have shown good answer to stimulate ES. A mixed crop of different species or a diversity gradient have a significant positive effect on yield, pollination, and weed/pest suppression (Isbell et al., 2017). However, trade-offs have to be carefully evaluated between high yield and biodiversity. Common inputs boost yield but reduce biodiversity and increasing biodiversity may well carry a yield cost. Though, it is possible to improve ES through a reasonable diversification (Isbell et al., 2017).

All ES are useful for agriculture. Garbach et al. (2014) describe 10 ESs particularly important for agriculture. Indeed, agriculture is based on a set of ES such as the class "hydrological services". As a result, they buffer the hydrological cycle and thus increase the infiltration of water into the soil, limit runoff and allow the transpiration of plants. Thus, it creates areas available to support agricultural production (Garbach et al., 2014). In addition, water purification through soil organisms being able to filter water of their contaminants is another hydrological service necessary for agriculture (Garbach et al., 2014). An Additional class of ES essential to the development of agriculture is the "Genetic resource" class. Biodiversity is a gene pool that supports natural and artificial selection. Thus, it allows the farmer to have cultivars that are more resistant to diseases and resilient to climate adaptation (Garbach et al., 2014). Finally, pest control, where pests are kept in check by natural enemies, is one more example of a class of ESs that are useful for agriculture. This reduces crop damage and reduces the need for pesticides and other interventions that harm the environment and human health (Garbach et al., 2014). This example demonstrates the importance of ES for agriculture. However, the set of ES essential for the proper functioning of agriculture are not yet fully described. Although science has made efforts to research critical ES such as pollination or biological control by studying a range of insect ES providers, other ES are still underestimated. This is the case for scavenger species which are ES providers of biotics and abiotic ES. The importance of scavenging in the food web has often been forgotten, with theoretical models based on plants, herbivores, and predators. (Wilson & Wolkovich, 2011). In the environment, scavenging contributes to the stabilisation of the food web due to the fact

that scavengers are generalists and very efficient, and hence actively participate in nutrient cycles (Wilson & Wolkovich, 2011). In other words, scavenger species can be considered as key guild in ecosystems but also as ES providers (Aguilera-Alcalá et al., 2020). On the one hand, they have an impact on other species such as plants by redistributing organic matter but also on other animal species by limiting the risk of spreading disease in the environment. The absence of scavenger species leads to a loss of biodiversity and biomass production, making them vitally important in many ecosystems (O'Bryan et al., 2018). On the other hand, all the benefits provided by scavengers directly and indirectly promote human welfare. They have effects on biotic and abiotic processes such as agricultural production or disease control, by consuming a large proportion of organic matter (O'Bryan et al., 2018). By consuming animal carcasses or human waste, vertebrate scavengers provide an organic matter regulation service. This reduces the risk of water contamination and saves money on waste management (O'Bryan et al., 2018). As for invertebrate scavengers, the effects of their activities have equally important implications.

Arthropods and ecosystem services

Today, arthropods represent 80% (\approx 1.3 million species) of the animal species known to science and their number is estimated at 5 to 10 million species (Culliney, 2013; Decaëns et al., 2006; Zhang, 2013). The groups that can be found in order of importance are Insecta, Arachnida, Crustacea, Trilobitomorpha and Myriapoda (Zhang, 2013). A major part of ES relies on arthropods, they play a crucial role in environments due to their diversity of form, function, diet, and ecological niches. Despite their small size, arthropods contribute to ES that are the most important for humanity such as pollination, biological control, soil structuration, and genetic resources (Culliney, 2013; Garbach et al., 2014). Today, it is 76% of crops are pollinated by insects (Klein et al., 2007); the value of the services provided by wild bees is estimated at \$518 billion per year (Raven & Wagner, 2021). Similarly, beneficial insects (predators, parasitoids) are likely to control up to 33% of crop pests, saving billions of dollars per year in the United States and worldwide (Power, 2010). Through adaptive strategies, it is possible to increase prey-predator interactions that can be stimulated to improve the effectiveness of pest population control.

Finally, arthropod populations have been under constant threat and disruption since the end of the Second World War. The example of bees is a striking one, the overall bee population (domestic and wild bees) are under pressure because of human activities. Intensive farming

practices, species invasion, habitat lost, insecticides and climate change are the main reasons for this decline and this fall affect ES (Meeus et al., 2018; Raven & Wagner, 2021). The most important ES provided by arthropods may be soil fertility. Indeed, arthropods have a real engineering power on soils. Their activities allow them to stir up a large quantity of soil between the different soil layers, thus providing exchangeable ions to the roots. Furthermore, the engineering work of ants and termites allows to aerate the soil and improve the water infiltration (Culliney, 2013). Finally, arthropod faeces help the organic matter to aggregate, which improves the structure of the soil, enhances water retention, and limits the leaching of nutrients (Culliney, 2013). In addition, they actively participate in the nutrient cycle by degrading plant and animal organic matter. They therefore have a direct effect on soil fertility by supporting the decomposition of organic matter and storing it directly in their tissues or by physically and chemically modifying the organic matter for other decomposers such as bacteria and fungi (Culliney, 2013).

The importance of scavenging and its underestimation

Trying to quantify the scavenging of arthropods on other arthropods is one way of highlighting the importance of these communities on our ecosystems, in particular on food webs and soil structuring. As a reminder, the terrestrial biomass of arthropods is estimated to be 0.2Gt of carbon. In comparison, the biomass of humans and their livestock is respectively 0.06 and 0.1 Gt of carbon (Bar-on et al., 2018). However, one of the difficulties in measuring the real impact of scavengers is that this behaviour may be opportunistic in some predatory arthropods (City & Carolina, 2020; Nelson et al., 2019). Therefore, when a predatory animal consumes a carcass, then it can be described as a facultative scavenger. Despite this, there are methods that can help differentiate predation from scavenging, one study (Zilnik & Hagler, 2013) presented an immunological approach that allowed to determine under laboratory conditions whether the prey was alive or dead when consumed. Thus, they were able to establish that a beetle (*Collops vittatus*) of the genus *Collops* was more a scavenger than expected. In the same idea, recent studies (Eubanks et al., 2019) suggest that the scavenging behaviour of ants is largely underestimated, and that ant scavenging is more important than previously thought. Through dominant and aggressive behaviour, ants monopolise carcasses by predated other arthropod scavengers and compete with vertebrate scavengers. The impact of ants can even slow down the rate of decomposition of carcasses (Holway & Cameron, 2021). Thus, ants would be the group that remove and consume most of the insect carcasses

in the terrestrial environments (Holway & Cameron, 2021). Similarly, Holway & Cameron (2021) believe that the energy obtained by ants through predation is overestimated compared to that provided by carcass scavenging, even though they point out the lack of information on this subject.

The goal of this work was to study scavenging arthropods of the macrofauna. It should be noted that the phylum of Mollusca through the group of Stylommatophora was also of interest to us in this study. Understanding the structure of food webs through arthropod interactions is of paramount importance for improving the understanding of soil-related ES. A more detailed description of scavenging contributes to a better understanding of the biotic mechanisms of nutrient redistribution in macrofauna. The consequences of climate change are still poorly known for these populations. Indeed, the available animal biomass seems to be decreasing due to human activity and climate change, which will have effects on scavengers, particularly because of the decrease in available carcasses. (Wilson & Wolkovich, 2011).

The aims of this work were (1) to measure scavenging rates in different habitats to determine the importance of this ES and how the habitat structure influence this ES, (2) to help understand the interactions between arthropods within the food web, and (3) to highlight the importance of macrofaunal communities for soil structuring.

Materials and methods

Study sites

Terceira, Azores, Portugal

The measurements were carried out in four habitats in the Azores, Terceira, Portugal. The island of Terceira is part of the Azores archipelago in the North Atlantic between 37° to 40° N latitude and 25° to 3° W. Terceira is the third largest island in the archipelago with a surface area of 400km², its highest point is at 1020m. The climate is a temperate oceanic climate characterised by a mild climate with low temperature variation, heavy precipitation strongly influenced by the topography of the island, high relative humidity, and strong winds (Reis,João; Dentinho, 2015). The island was colonised in the mid-15th century, since then human activities have profoundly altered the local ecosystems. In 2009, 58% of Terceira's total land area was utilised for agriculture (mainly grass and fodder crops). Temporary crops were the most popular land use (43.1%) followed by permanent pasture (16.4%). Other land

uses included vineyards (0.3%), orchards (0.6%), other agricultural properties (0.5%), forests (4.8%) and other places (0.8%) (Reis & Rodrigues, 2017). Thus, the main economic sector of the island is the production and processing of dairy products (Reis, João; Dentinho, 2015).

The habitats

Orchards

Part of the measurements were carried out in orchards belonging to two producers. The first one "Bica" was an orchard of about 4.6Ha growing mainly banana (*Musa sp.*) and oranges (*Citrus x sinensis*). Conventionally managed, the orchards were managed with pesticides for pests and diseases, fertilisers, and herbicides to eliminate grass cover. Two plots of 0.06Ha were selected for the study (Table 1). The second orchard, "San Bartolomeu", was a citrus (lemon and orange) production of 0.14Ha. Production was not managed conventionally, with no application of pesticides and no removal of grass cover here too, two plots were selected for the study (Table 1).

Vineyards

The vineyards were mainly located in Biscoitos, Azores Portugal (38°47'32"N 27°15'32"W) near the sea. In the XV century, the Portuguese introduced the vine culture to the Azores during its colonisation. Astorian vineyards were generally located in low-lying areas on basaltic lava fields that were divided into small enclosures protected from sea winds by stone walls (Madruga et al., 2015). The vines were pruned to be relatively close to the ground to limit their exposure to the wind and to increase the efficiency of the walls. All vineyards in this study were intensively managed for wine production. The first vineyard, Simas, was part of a cooperative in Adegas, (Table 1), two randomly selected plots of 60m² and 180m² were chosen for the experiments. The second site "Coop GR" (Table 1) had the same characteristics as the first site. Two plots of 330m² and 55m² on two different nearby vineyards were chosen.

Native forest

Most of the remaining native forests on the island were within the protected area network. These three protected areas were located in the northern part of the island at altitudes above

500m since historical human activity cleared these forests. They are characterised by high humidity and small evergreen trees (Borges et al., 2017). The dominant trees and shrubs were the endemic species *Juniperus brevifolia*, *Erica azorica*, *Laurus azorica* and *Ilexperado azorica*. Sometimes, when conditions were wetter, the Azorean cedar (*J. brevifolia*) was more abundant (Borges et al., 2017). These native forests were lush and include bryophyte communities on all substrates (Borges et al., 2017). Four sites were chosen for their accessibility, 3 sites “Junglecross”; “Stoneage”; “Matela”, (Table 1) close to the reserve Ferraria Biscoito Partial Natural Forest Reserve (38°45'22 "N 27°12'59 "W) and one site “Cedrorum” further south near a smaller piece of forest.

Urban areas

The selected sites were near the University of the Azores (38°45'32 "N 27°13' 55 "W). These sites were regularly maintained (lawn mowing) and managed by human activity. The four sites were located within the faculty (Table 1).

Flakkebjerg, Zealand, Denmark

The other part of the study was carried out in Zealand, Flakkebjerg (55°19'45" N 11°23'56" E) Denmark. The Zealand area covered an area of 9060 km² and was characterised by intensive agriculture with cereal crops (almost exclusively wheat and barley). During the last 10 years, the total rainfall in Slagelse (55°24'10 "N, 11°21'14 "E) was 581mm and the average temperature recorded for the same period was 10°C with an average maximum temperature of 30°C and an average minimum temperature of -10°C (Danish Meteorological Institute).

The habitats

Wheat field

The fields selected for the study were wheat fields (*Triticum* spp). The crops were intensively managed and follow a classical technical itinerary. Four sites have been selected (Table 2).

Field edges

The selected field edges were close to a wheat and beet field. The measurements were made on four sites (Table 2).

Native forest

The native forest of Sorø (55°22'44 "N 11°33'36 "E) had the advantage of being preserved from human activities even though there were hiking trails. It is mainly made up of beech trees (*Fagus sylvatica*) and the dead wood was not removed. The forest was bordered by pastureland except for its southern border which was bordered by a lake and its area was 29.2Ha. The experiments were carried out on four sites in the forest (Table 2).

Urban areas

The sites were selected within the perimeter of the Flakkebjerg Research Centre campus (55°19'45" N 11°23'56" E) (Table 2).

Measurement of scavenging rates

Scavenging rates were measured by the sentinel approach, similar to that of Tolonen (1995). Patches of dead insects were "modelled" by gluing dead larvae of the house fly (*Musca domestica*) onto cardboard squares. Ten fly larvae in the L2-L3 stage were glued in a regular pattern on cardboard squares (6 cm x 4.5 cm) using white glue ("Supertite" in Portugal and "Skolelim" in Denmark). These glues have been selected for their neutrality, i.e., they did not attract arthropods because of their constituting chemical compounds. A drop of glue was applied to the cards with the end of a toothpick (See annex "pilots test" for all pilot experiments). A card was placed face down near the soil, held in place by two toothpicks so that the card surface stayed 1 to 2 cm above the soil surface. During the day, 15 cards were set up at four sites and during the night 15 cards were set up at two sites. Each card was placed 5 m apart from each other to ensure independence of results. The exposure time was 10 hours during the day and between 6 and 10 hours at night. Every two hours, each card was turned over to count the number of larvae that had been scavenged. Larvae that were missing, partially eaten and those that were emptied from the inside were scavenged. For each the scavenging rate was calculated by dividing the number of scavenged larvae by the number of larvae initially present.

Exclusion of mammals

The "mammal exclusion" experiment was part of a series of pilot experiments performed to standardise the method of measuring the scavenging rate. (See annex "pilot test"). A plastic box was used in which in all four sides, an 8 cm x 6 cm window was cut at bottom level. Over these windows, a net (mesh size 2 cm x 2 cm) was fixed with strips of sticky tape. This mesh size was chosen to prevent small mammals from accessing the bait but allowing arthropods to pass through without difficulty. Finally, the box was firmly anchored to the ground with two metal rods. Other cards without the exclusion system were placed 1m away. Three normal and three "exclusion system" cards were placed per site. Experiments were carried out at four sites in San Bartolomeu and Bica on ground with no vegetation for 24 hours.

Breeding of Fly larvae

The use of fully grown *Musca domestica* larvae as sentinels to characterise scavenging intensity was justified for several reasons. *M. domestica* had a relatively fast development cycle and is easy to rear when placed under optimal temperature conditions. Finally, it was easy to observe the results in the field. Indeed, it was simple to see visually if the larvae have been consumed, unlike the pupae which require the use of a binocular (Tolonen, 1995). The fly colony was obtained from a culture maintained at Aarhus University, Flakkebjerg Research Centre, near Slagelse, Zealand.

For the experiments on Terceira, we established a local culture using pupae obtained from the culture in Denmark. The flies were bred in wood cages. Following the recommendation by (Pastor et al., 2011) that flies should have a space of 56.8 cm³, one cage contained approximately 30 adult flies. The adults were fed with a mixture of milk powder (500 g), icing sugar (500 g) and yeast (10 g) (Fletcher et al., 1990). This mixture was placed in a Petri dish inside the cages. Water was provided using a 100 ml plastic tube sealed with cotton to allow the water to diffuse by capillary action. To stimulate fly reproduction, a strip of 4 cm by 4 cm of tissue paper soaked in milk was placed in a plastic container in the cage. The flies laid their eggs on the paper. The system was replaced every week. The sheet of paper with the eggs was placed on top of the containers containing the larval growth medium.

The larval medium consisted of the following: 10 g yeast, 15 g malt, 200 g dried, ground alfalfa, 400 g of wheat bran and 1.3 L of water. The mixture was prepared in a large (volume 3690 cm³) container before being distributed to smaller ($v = 680 \text{ cm}^3$) ones. After the egg

stage, there are 3 stages of larval development, 3-5 days later the larvae pupate for 4-5 days, then the adults emerged. The cycle is 7-10 days under ideal temperature conditions around 26°C (Čičková et al., 2015). Larvae that reached the L2-L3 stage were collected every 2 days and stored in a freezer at -18°C until use.

Statistical analysis

We used GLMMs with binomial distribution to estimate the probability of scavenging at the end of the experiments, i.e., 18h, 24h and 8h. On the other hand, we estimated the probability of scavenging as a function of time, i.e., the dynamics of scavenging with a Cox regression. The data were transformed so that each scavenging event was represented by a "1" and each non-scavenging event by a "0" for all hours and all cards. A total of 58500 data were processed. The data were processed with the statistical software R (R Core Team (2020). R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>) through RStudio.

Results

General results

The data indicates that the average scavenging rate for all experiments was 47.3% (sd= 42.7%, n= 1470). The scavenging rate in Terceira (orchards, vineyards, urban areas, and native forests) was 64.5% (sd= 40.7%, n= 750), while that in Denmark (wheat fields, field edges, urban areas, and native forests) was 29.5% (sd= 37.1%, n= 720).

Habitat differences

Habitats, Terceira

On Terceira, the scavenging rate in the vineyards was 97.7% (sd=11.8%, n= 180); the scavenging rate in the orchards was 67.8% (sd= 40.4%, n= 180); the scavenging rate in the urban areas was 68.7% (sd= 39.2%, n= 180); and the native forests was 29.5% (sd= 29.9%, n= 210)

Habitats, Denmark

In Denmark, the scavenging rate in the native forests was 53.6% (sd= 37.1%, n= 180); field scavenging rate was 41.7% (sd= 39.9%, n= 180); urban areas scavenging was 13.6% (sd= 26.9%, n= 180); and field edges had a scavenging rate of 9% (sd= 20.7%, n= 180).

Day-Night differences

The overall measured scavenging rate during the day was 40.1% (sd= 43%, n= 960); and the overall scavenging rate at night was 60.9% (sd= 38.5%, n=510).

Terceira

On Terceira, the daytime scavenging rate was 60.9% (sd= 42.6%, n= 480) and the scavenging rate measured at night was 70.8% (sd= 36.1%, n= 270).

Terceira Habitat Day

The scavenging rates measured during the day were 98.2% (sd= 10%, n= 120) in the vineyards; 71.8% (sd= 40.9%, n= 120) in the in orchards; 54.8% (sd= 41%, n= 120) in the urban areas; and 18.8% (sd= 22.7%, n= 120) in the native forests.

Terceira Habitat Night

The scavenging rate measured at night were 96.7% (sd= 14.8%, n= 60) in the vineyards; 96.3% (sd= 10.1%, n= 60) in the urban areas; 59.7% (sd= 38.5%, n= 60) in the in orchards; and 43.9% (sd= 32.3%, n= 90) in the native forests.

Denmark

The daytime scavenging rate in Denmark was 19.3% (sd= 32.2%, n= 480); The scavenging rate measured at night in Denmark was 49.8% (sd= 38.2%, n= 240).

Denmark Habitat Day

The scavenging rate measured during the day in Denmark in the forest was 40.1% (sd= 33.5%, n= 120); the scavenging rate in fields was 29.1% (sd= 37.6%, n= 120); the scavenging rate in the urbans areas was 5.4% (sd= 19.1%, n= 120); and the scavenging rate in edge fields was 2.8% (sd= 14.8%, n= 120).

Denmark Habitat Night

The scavenging rate measured at night in Denmark in forest was 80.7% (sd= 27.9%, n= 60); the fields was 66.8% (sd= 31.8%, n= 60); the scavenging rate in the urban areas it was 30.0% (sd= 32.3%, n= 60); and in the edge fields the scavenging rate was 21.5% (sd= 24.8%, n= 60).

Occasional observations of scavengers

During the various assessments, 1794 direct observations of scavengers were made, and 14 groups of arthropods were identified. This information is incidental and must be taken with a certain amount of caution. Therefore, in this study, it has only an informative value and will not be the subject of further statistical analysis.

Scavengers in Terceira

The average number of arthropod groups observed on the cards in all habitats was 6.25 (sd= 3.1, n=4). We observed a total of 12 groups of arthropods during the checks. 1549 direct observations of arthropods were made during the checks, Formicidae with 62% of the observations represented the majority, followed by Collembola with 21% of the observations. Then the class of Gastropoda (slugs and snails) which accounts for 8% of observations. Finally, the Isopoda with 5% of the records. The other data are the Opiliones 2%, and the Dermaptera 1%. The rest are completed by Diptera, Diplopoda, and Chilopoda, all <1%.

Habitat variation

The habitat with the highest diversity was the orchards with 9 groups of arthropods recorded. In contrast, the habitat with the lowest diversity was the vineyards with only 2 groups observed. 8 groups were observed in native forests and 6 in urban areas. The main scavengers were ants, ranging from 81% to 99% of observations in all habitats apart from for the native forests where they do not appear in our records. Collembola were the only arthropods found in all habitats, although they remained in a very small minority, never exceeding 1% in any habitat except the native forests, where they accounted for 68% of the observations.

Day Night variation

On average, we observed 2.75 groups (sd= 1.5, n=4) during the day and 5.5 groups (sd= 3.1, n=4) at night. Some families were only present at night, such as slugs and isopods in orchards, whereas they were observed during the day and night in other habitats, such as native forests and urban areas. Other groups such as Collembola were present only at night, only during the day and night and day depending on the habitat. However, the pattern of observations between day and night remains the same, mainly due to the overwhelming role of the ants. Although there were more observations during the day (899) than at night (650), Formicidae were still in the majority at night, going from 74% of observations during the day to 46% at night. The same idea, for Collembola, which accounts for 28% of observations at night compared to 16% at day. The share of Gastropoda increased from 7% during the day to 10% at night and Isopoda from 3% during the day to 8% at night. Dermaptera and Opiliones

were not observed during the day, accounting for 2% and 4% of observations at night respectively.

Scavengers in Denmark

The average number of arthropod groups observed in the habitats in Denmark was 3.25 (sd= 2.22, n=4). In total 7 different arthropod groups were observed out of 245 during the checks. Of the 245 direct observations, Formicidae accounted for 56% of the total, followed by Isopoda at 10%. Dermaptera and Opiliones were at 9% and slugs at 8%. Finally, beetles and spiders represented respectively 5% and 3% of the total observations.

Habitat variation

The habitat with the highest diversity was the primary forest with 6 arthropod groups recorded, the one with the lowest diversity was the edge field with only 1 family. The main scavengers were ants, between 94% and 54% of observations in all habitats, except for wheat fields where they were not recorded. In the wheat fields, beetles were the main scavengers noted with 59% of the observations.

Probability of scavenging

Probability of scavenging in Terceira

The best model for Terceira included the interaction between the habitat and the time of the day (site and card were used as random factors). Scavenging rates in the vineyards during the day and at night were not significantly different ($p=0.203$). During the day, scavenging rates in the vineyards were significantly higher than in the orchard and urban sites ($p<0.001$ for both), while at night no significant difference was observed ($p=0.147$ for the vineyard-orchard comparison, and $p=0.968$ for vineyard-urban sites). Scavenging rates in the orchards during the day and at night were not significantly different ($p=0.999$). During the day, scavenging rates in the orchards were significantly higher than in the urban sites ($p=0.05$), while the opposite was true at night ($p=0.002$). Scavenging rates in the urban sites during the day were significantly lower than at night ($p<0.001$), and the same was found in the native forest ($p=0.029$). Scavenging rate in the forests was significantly lower than in vineyards and orchards ($p<0.001$ for both, during the day and at night) and the urban areas ($p=0.001$ during the day, $p=0.04$ at night).

Probability of scavenging in Denmark

The best model for Denmark included only the habitat and time of

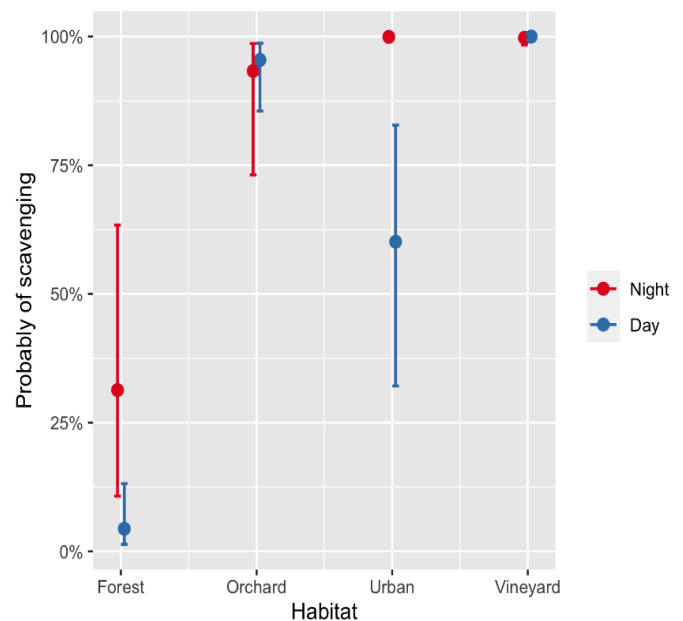


Figure 1: Probability of scavenging in Terceira. Graph representing the probability of a larva being scavenged as a function of habitat during the day and night. The plots represent the mean \pm 95% confidence

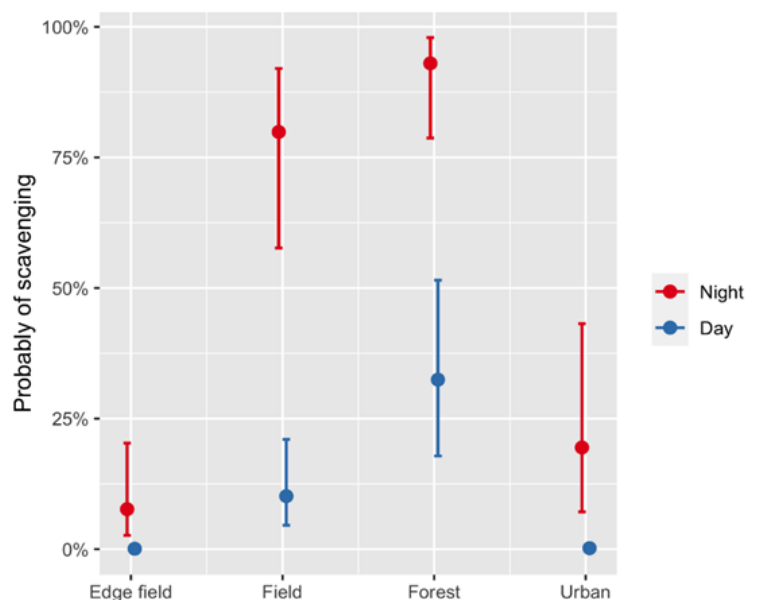


Figure 2: Probability of scavenging in Denmark. Graph representing the probability of a larva being scavenged as a function of habitat during the day and night. The plots represent the mean \pm 95% confidence interval.

the day as independent factors (site and card were used as random factors). Scavenging rate during the night was significantly ($p < 0.001$) higher than during the day. Scavenging rate at the field edges were significantly lower than in the field or the forest ($p < 0.001$ for both). Scavenging rate in the urban habitat was significantly lower than in the wheat fields and the forests ($p < 0.001$ for both). No significant difference was observed between scavenging rates at the field edges and the urban habitat ($p = 0.345$), nor between the wheat fields and the forest habitats ($p = 0.115$).

Scavenging difference between Terceira and Denmark

The best model for the countries together included the interactions between the habitat and country and the habitat and the time of the day (site and card were used as a random factor). Scavenging rates in the forests were significantly higher in Denmark than in Terceira ($p = 0.0039$), while the opposite was true for urban sites ($p < 0.001$). Scavenging rates were significantly lower during the day than at night in both the forest and urban sites in both countries ($p < 0.001$ for both).

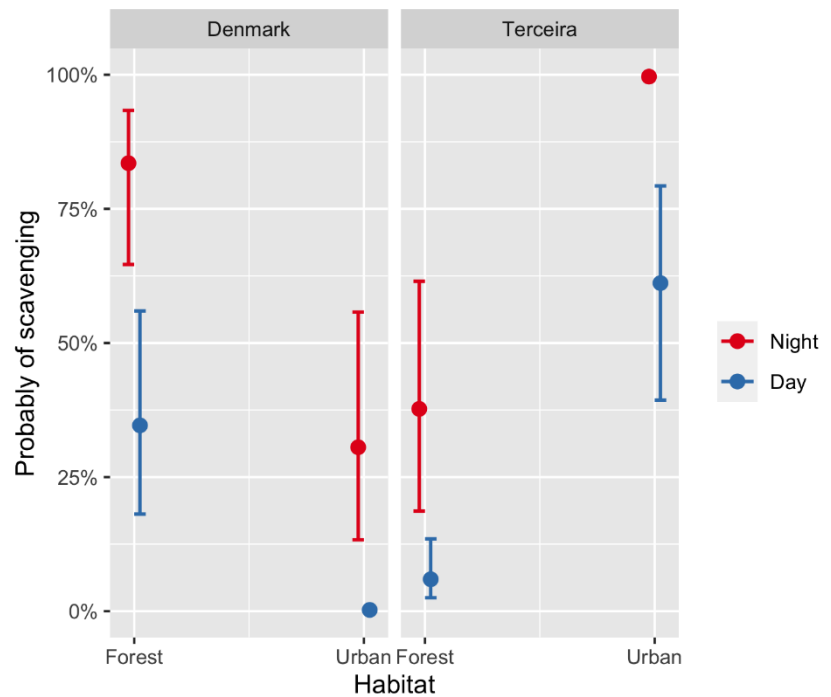


Figure 3 : Probability of scavenging in Terceira and Denmark. Graph representing the probability of a larva being scavenged as a function of habitat during the day and night. The plots represent the mean \pm 95% confidence interval.

The dynamics of scavenging

Comparison between countries

The scavenging dynamics showed a statistically significant difference between the two countries ($p < 0.001$). The fastest rate of disappearance of exposed larvae was observed in Terceira, both during the day and at night.

Comparison between habitats

Terceira, day

In Terceira, the day Scavenging dynamics showed a statistically significant difference in all habitats (Chisq= 3428; $p < 0.001$). The same is true for the comparison between the habitats Orchards, Urbans and Forests, which was statistically significant (Chisq= 933; $p < 0.001$), as well as the comparison Forest-Urban (Chisq= 574; $p < 0.001$) and Vineyards-Orchards (Chisq= 1126; $p < 0.001$). (See figure 4).

Terceira, Night

At night, the overall scavenging dynamics also showed a statistically significant difference in all habitats (Chisq= 1831; $p < 0.001$). The habitat vineyards had the highest scavenging dynamics with the lowest larval survival values. The comparison between the habitats Orchards, Urban areas and Forests was also statistically significant (Chisq= 1022; $p < 0.001$), as was the comparison Forest Orchards (Chisq= 58.5; $p < 0.001$). Finally, there was no statistically significant difference between Vineyards Urbans (Chisq= 5.6; $p < 0.018$). (See figure 5).

Denmark, Day

Scavenging dynamics showed a statistically significant difference in all habitats (Chisq= 427; $p < 0.001$). So did the comparison between Edge-Fields, Urbans and Fields which was statistically significant (Chisq= 267; $p < 0.001$). However, the Urbans and Edge-Fields habitats showed a non-significant difference in survival dynamics (Chisq= 1.7; $p < 0.19$) as did the Forests and Fields habitats (Chisq= 1.1; $p < 0.30$). (See figure 6).

Denmark, Night

The scavenging dynamics showed a statistically significant difference in all habitats (Chisq= 571; $p < 0.001$). The same is true for the comparison between Edge-Field, Urban and Field

habitats which was statistically significant (Chisq= 282; $p < 0.001$). Furthermore, the Urbans and Edge-fields habitats showed a significant difference in survival dynamics (Chisq= 8.7; $p < 0.003$). In contrast, forest and fields habitats showed a significant difference in their scavenging dynamics (Chisq= 1.1; $p < 0.30$). (See figure 7).

Comparison of country habitats

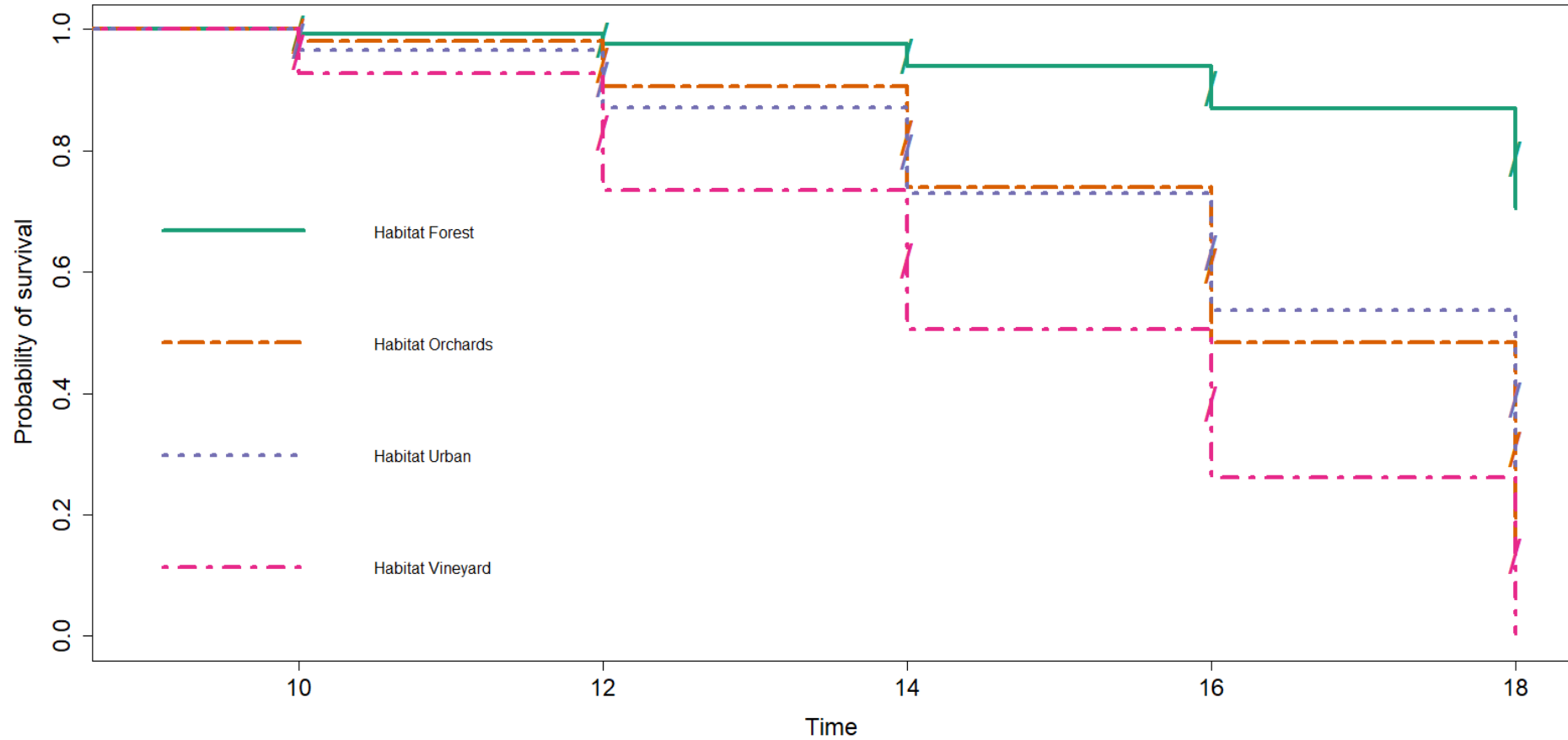
Forest

Finally, the scavenging dynamics of the forest habitat by country showed very strongly significant differences (Chisq= 66.2; $p < 0.001$) during the day and (Chisq= 541; $p < 0.001$) at night (Figures 8, 10).

Urban

The comparison of Urban habitats scavenging dynamics by country showed very strongly significant differences (Chisq= 912; $p < 0.001$) during the day and (Chisq= 1527; $p < 0.001$) at night (Figures 9, 11).

Probability of survival from scavenging as a function of time, Day, Terceira



1 *Figure 4 : Cox regression, the curves indicate the dynamics of scavenging, the day in Terceira. The probability of survival in the vineyards is 93% (SE = 3.3%) at*
 2 *10h, 73% (SE = 6%) at 12h, 51% (SE = 7%) at 14h, 26% (SE = 6.3%) at 16, and 0.5% (SE = 1%) at 18h. The probability of survival in the orchards is 98% (SE =*
1.8%) at 10h, 91% at 12h (SE = 4.1%), 74% at 14h (SE = 6.7%), 48% at 16h (SE = 8.4%), and 14% (SE = 6.7%) at 18h. The probability of survival in urban areas
is 97% (SE = 2.4%) at 10h, 87% (SE = 4.7%) at 12h; 73% (SE = 6.6%) at 14h; 54% (SE = 8.2%) at 16h; and 24% (SE = 8.6%) at 18h. The probability of survival in
Forest is 99% (SE = 1.1%) at 10h, 98% (SE = 2.2%) at 12h; 94% (SE = 3.7%) at 14h; 87% (SE = 6.1%) at 16h, and 71% (SE = 11%) at 18h.

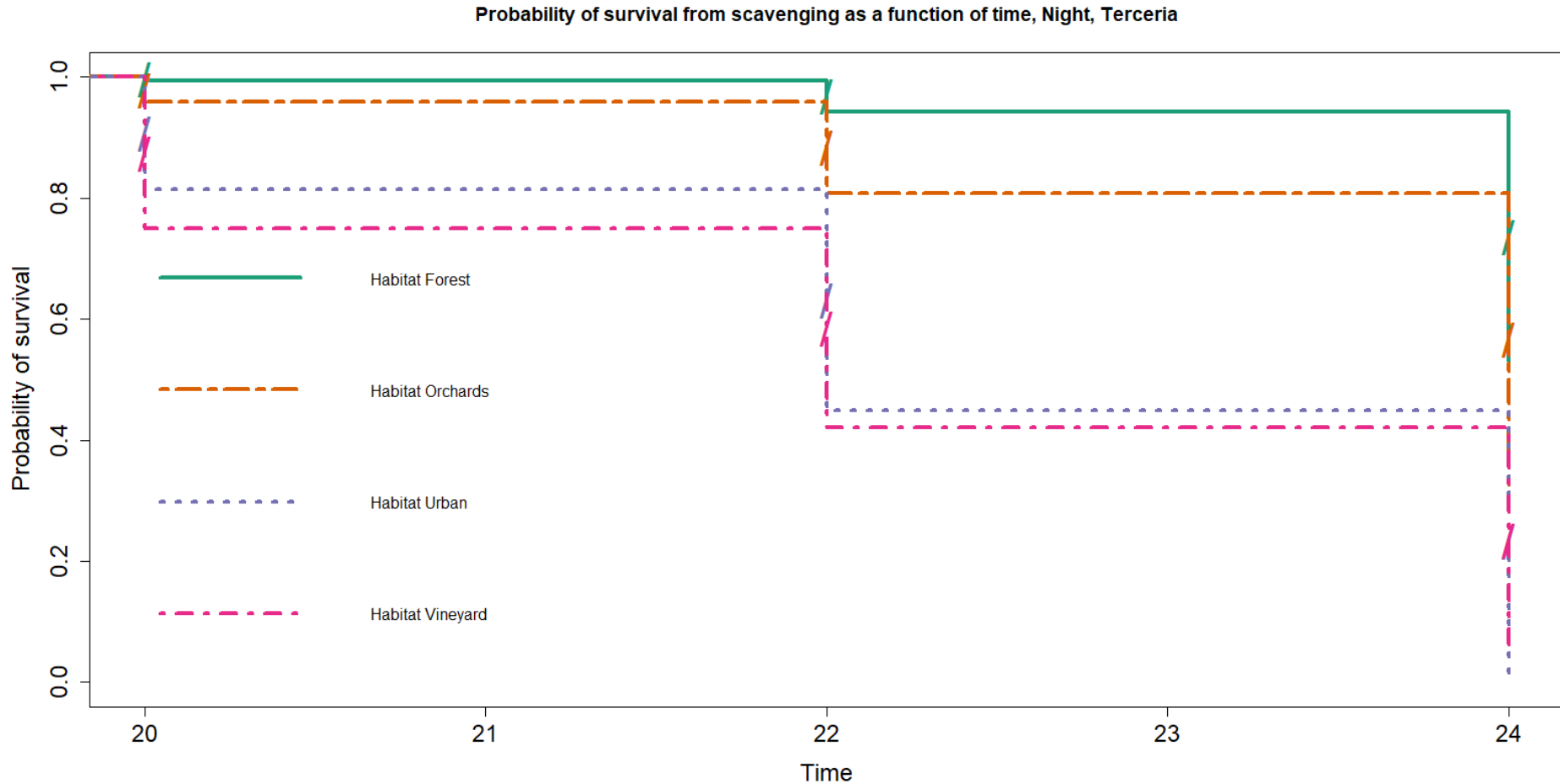


Figure 5 : Cox regression, the curves indicate the dynamics of scavenging, the night in Terceira. The probability of survival in the vineyards is 75% ($SE = 1\%$) at 20h, 42% ($SE = 1.2\%$) at 22h, and 49% ($SE = 0.6\%$) at 24h. The probability of survival in the orchards is 96% ($SE = 0.5\%$) at 20h, 81% at 22h ($SE = 1.1\%$), 33% ($SE = 1.6\%$) at 24h. The probability of survival in urban areas is 82% ($SE = 0.9\%$) at 20h, 45% ($SE = 1.2\%$) at 22h; 1.7% ($SE = 0.3\%$) at 24h. The probability of survival in native forest is 99% ($SE = 0.2\%$) at 20h, 94% ($SE = 0.05\%$) at 22h; 53% ($SE = 1.6\%$) at 24h.

Probability of survival from scavenging as a function of time, Day, Denmark

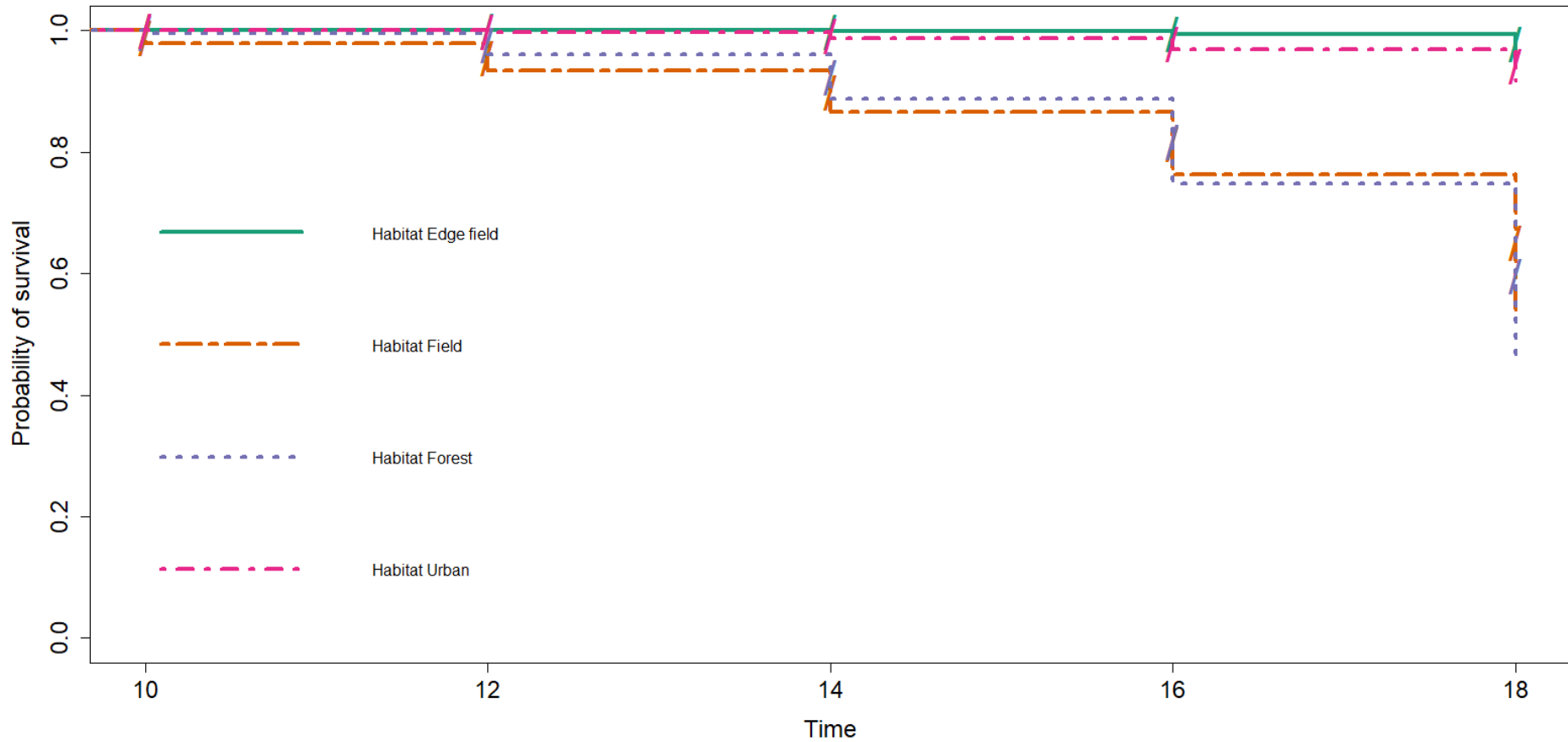


Figure 6 : Cox regression, the curves indicate the dynamics of scavenging, the day in Denmark. The probability of survival in the forest is 99% (SE = 0.01%) at 10h, 96% (SE = 0.3%) at 12h, 89% (SE = 0.5%) at 14h, 74% (SE = 0.8%) at 16, and 45% (SE = 1.2%) at 18h. The probability of survival in the fields is 98% (SE = 0.2%) at 10h, 99% at 12h (SE = 0.3%), 87% at 14h (SE = 0.5%), 76% at 16h (SE = 0.8%), and 54% (SE = 1.1%) at 18h. The probability of survival in urban areas is 100% (SE = 0%) at 10h, 100% (SE = 0.07%) at 12h; 99% (SE = 0.2%) at 14h; 97% (SE = 0.3%) at 16h; and 92% (SE = 0.7%) at 18h. The probability of survival in edge field is 100% (SE = 0%) at 10h, 98% (SE = 0.02%) at 12h; 100% (SE = 0.04%) at 14h; 99% (SE = 0.2%) at 16h, and 97% (SE = 0.5%) at 18h.

Probability of survival from scavenging as a function of time, Night, Denmark

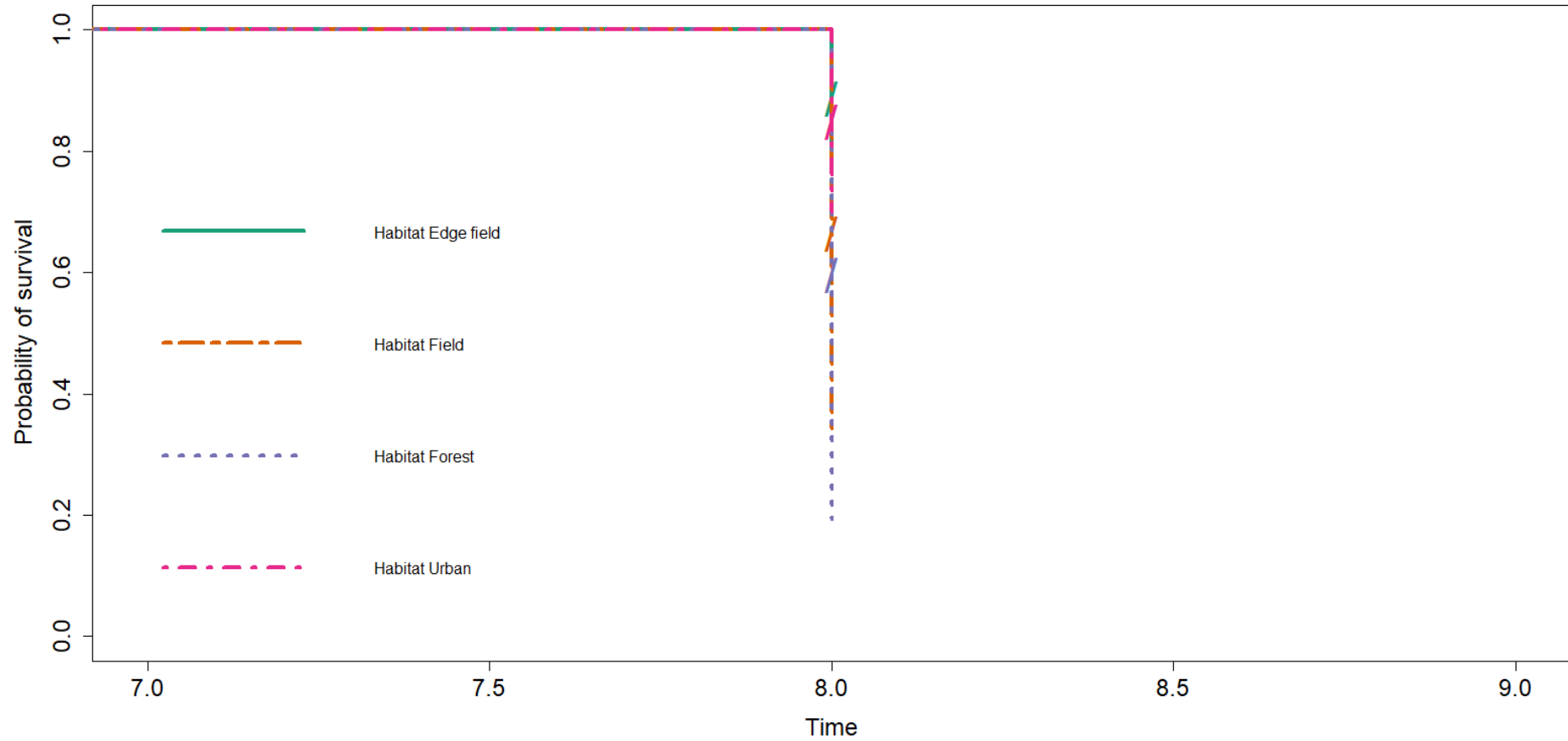


Figure 7 : Cox regression, the curves indicate the dynamics of scavenging, the night in Denmark. The probability of survival in the forest is 20% (SE = 1.6%) at 8h. The probability of survival in the fields is 33% (SE = 1.9%) at 8h. The probability of survival in urban areas is 70% (SE = 1.9%) at 8h. The probability of survival in edge field is 78% (SE = 1.7%) at 8h.

Probability of survival from scavenging as a function of time, Day, Forest

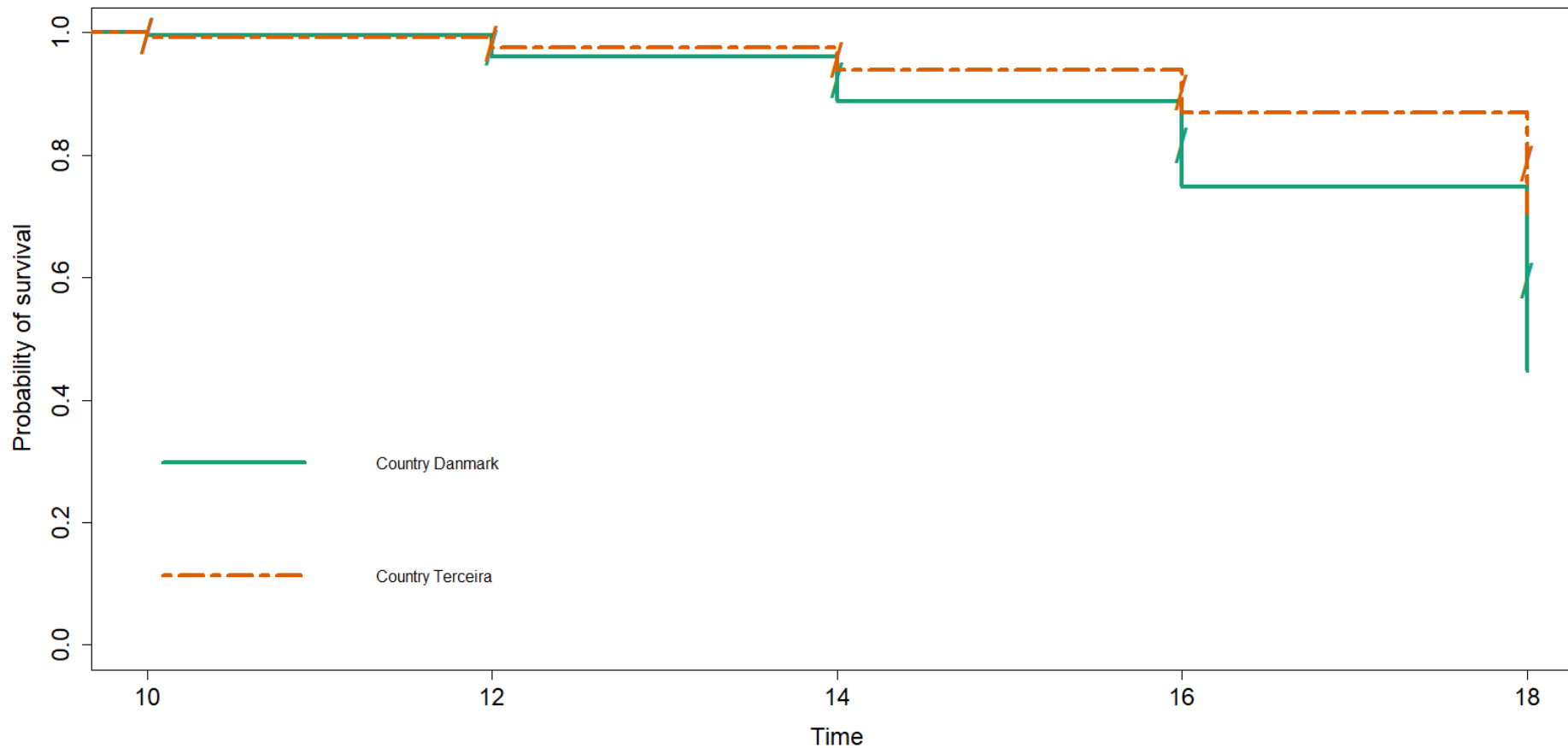


Figure 8 : In the Forest, the probability of survival of larvae in Terceira is 99% (SE = 1.1%) at 10h, 98% (SE = 2.2%) at 12h; 94% (SE = 3.7%) at 14h; 87% (SE = 6.1%) at 16h, and 71% (SE = 11%) at 18h. The probability of survival of larvae in Denmark in forest is 99% (SE = 0.01%) at 10h, 96% (SE = 0.3%) at 12h, 89% (SE = 0.5%) at 14h, 74% (SE = 0.8%) at 16, and 45% (SE = 1.2%) at 18h.

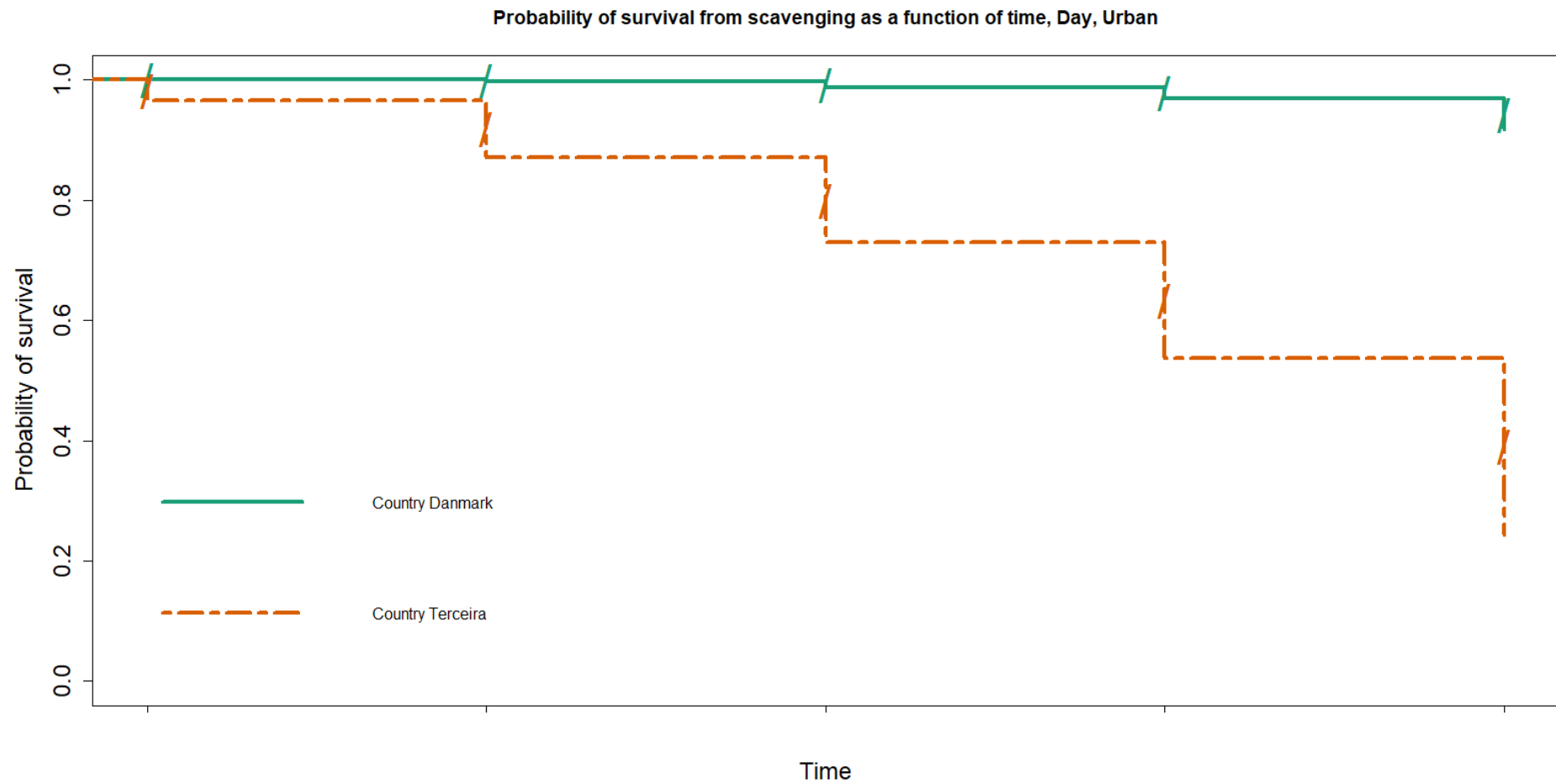


Figure 9 : In urban areas, the probability of survival of larvae in Terceira is 97% (SE = 2.4%) at 10h, 87% (SE = 4.7%) at 12h; 73% (SE = 6.6%) at 14h; 54% (SE = 8.2%) at 16h; and 24% (SE = 8.6%) at 18h. The probability of survival of larvae in Denmark is 100% (SE = 0%) at 10h, 100% (SE = 0.07%) at 12h; 99% (SE = 0.2%) at 14h; 97% (SE = 0.3%) at 16h; and 92% (SE = 0.7%) at 18h.

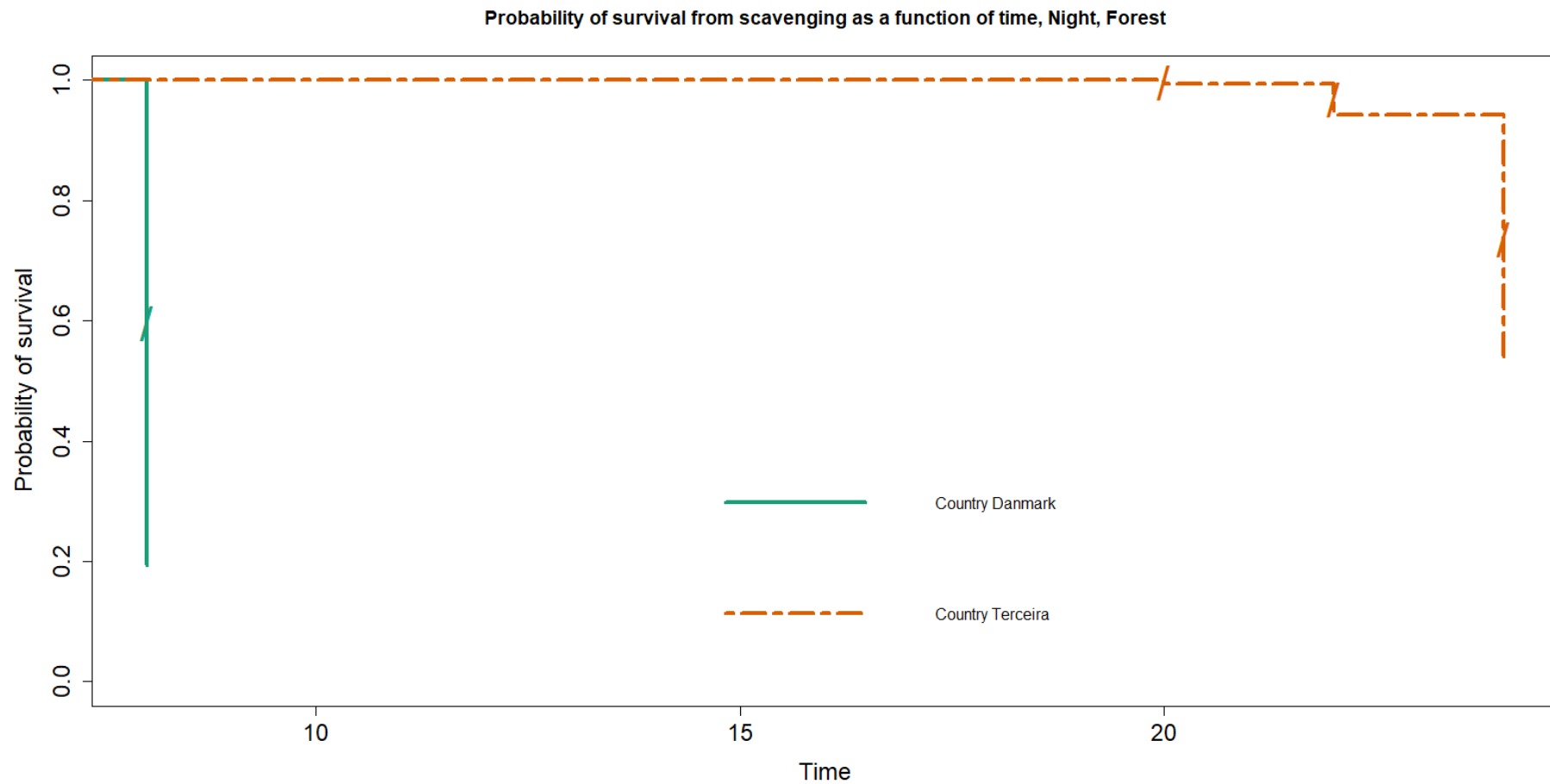


Figure 10 : The night, in Forest, the probability of survival of larvae in Terceira is 82% (SE = 0.9%) at 20h, 45% (SE = 1.2%) at 22h; 1.7% (SE = 0.3%) at 24h. The probability of survival of larvae in Denmark in urban areas is 20% (SE = 1.6%) at 8h

Probability of survival from scavenging as a function of time, Night, Urban

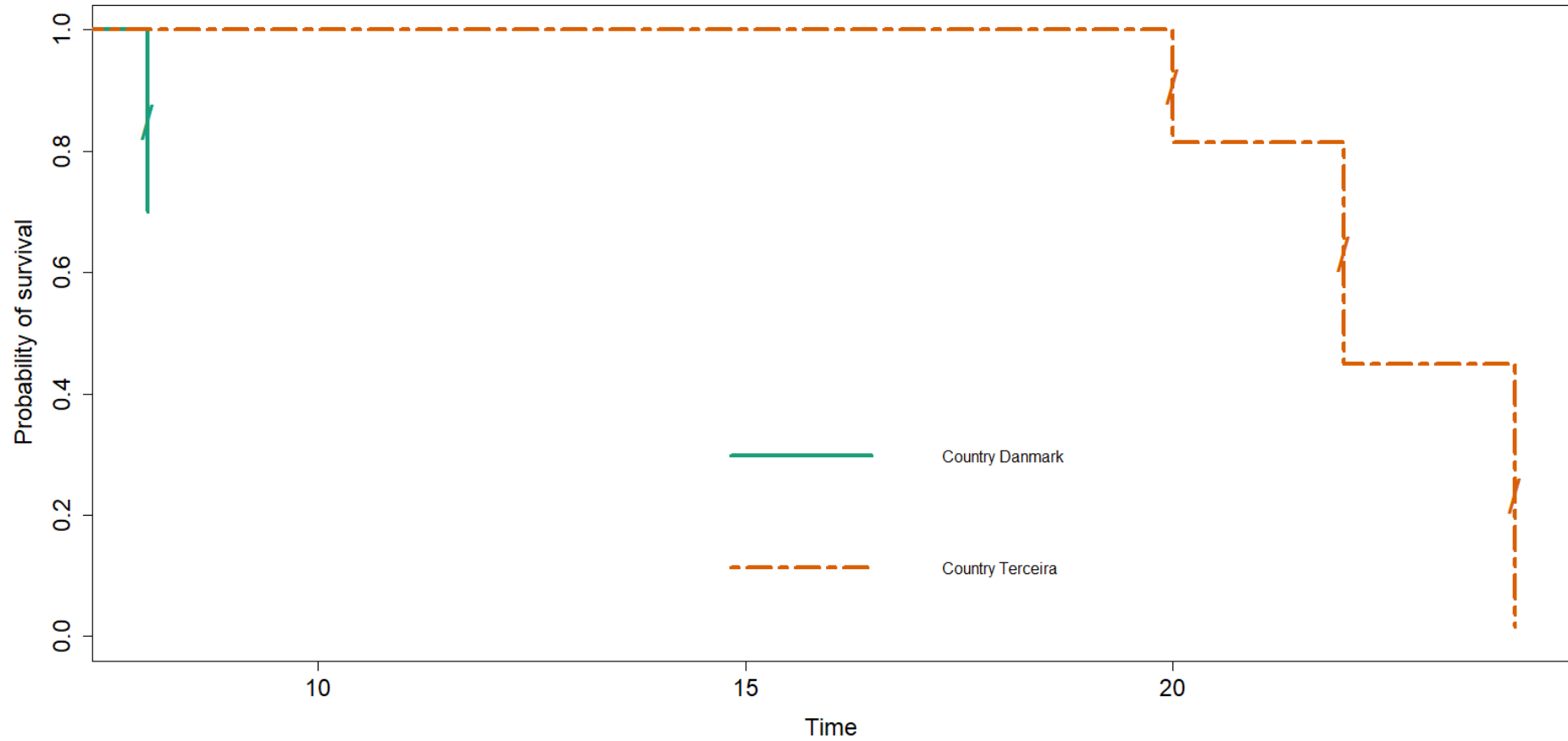


Figure 11 : The night, in urban areas, the probability of survival of larvae in Terceira is 99% (SE = 0.2%) at 20h, 94% (SE = 0.05%) at 22h; 53% (SE = 1.6%) at 24h. The probability of survival of larvae in Denmark in urban areas 70% (SE = 1.9%) at 8h

10

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Discussion

These results should be considered as an approximation of the carrion removal levels over a 24-hour period. Overall, these results showed relatively high levels of scavenging in the two regions studied. Indeed, due to the lack of knowledge on the subject, we expected that the scavenging behaviour, i.e., the scavenging rate and dynamics, would be lower in the different modified habitats with respect to the original ones which were forests both in Terceira and Denmark.

Scavenging is an understudied phenomenon and ecosystem service, so part of this work was simply to obtain quantitative, comparable data about the existing scavenging intensity in various modified habitats in cultivated landscapes. Unexpectedly, the level of scavenging was found to be high. Furthermore, our predictions that the type of habitat could influence the level of scavenging but less than in the original ones, were not supported in an island setting but were supported in northern Europe (Denmark).

The structure of the habitats seems to be an important factor influencing the scavenging behaviour as well as the day-night cycle. The habitat structure considered in this work is based on visual observations of the different types of environments. In particular, the density of the vegetation and the spatial organisation of the habitat, including the presence or absence of patches, and the different vegetation strata. For example, native forest has a high vegetation density and a relatively closed vegetation layer of about 2.5m without patches, compared to orchards which have a lower vegetation density and a much less dense and open vegetation layer of about 2.5m and patches. Vineyards are highly fragmented with no vegetation layer and a low vegetation density. Finally, urban areas were completely open, only grass, without vegetative layer and no plots. In Denmark, the wheat fields were patchy and densely vegetated when the crop grew. The native forest had a relatively low vegetation density compared to the forest in Terceira. However, it had a first vegetative layer of about 15-20m and a second one of about 2m (bush). In addition, the presence of an important layer of humus is to be noted. The field edges and the urban areas did not have any vegetation layer or plots.

Terceira

Terceira showed a high level of scavenging in general, with an average scavenging rate of 65.5%. This translated into a high probability of larval scavenging and a high scavenging

dynamic. Variations could be observed between habitats. The habitat with the lowest level of scavenging was the native forest. By contrast, the habitat with the highest level of scavenging were the vineyards. During the day, the scavenging was lower in all habitats than at night. The low scavenging levels in the native forests were a surprise as well as the high levels in anthropic environments. The habitats studied showed that they had their own level of scavenging that was most certainly correlated with the community of arthropod scavenger populations they supported. This seems to be in line with several studies, as scavenging insect populations are influenced by habitat structure (Alvarado-Montero et al., 2021). Similarly, a higher fragmentation of the territory can offer a higher diversity of habitats (Fahrig, 2017). Finally, habitats with a lower vegetation density are more favourable for scavenging species because it is easier for them to detect available carcasses (Braack, 1987). In fact, it was possible to clearly differentiate between two types of environments, anthropic environments with human activity such as vineyards, orchards, and urban areas and non- anthropic environments such as the native forest. Anthropic habitats were more likely to have a higher scavenging rate than non- anthropic habitats. This may mean that the scavenger arthropod species present in these environments were more generalist and better at exploiting the carcasses. Due to the insular nature of Terceira, it is possible that scavenging arthropods were not present before the arrival of man in the original habitats. Other hypotheses that may explain such a difference are better detection of carcasses in these environments that were less dense, particularly in terms of vegetation, better exploitation of the resource and/or a higher density of scavenger arthropod species. Our direct observations seemed to point in this direction.

Denmark

In Denmark, I recorded an overall more moderate level of scavenging, with a scavenging rate of 29% across all experiments. Nevertheless, a notable difference is that in Denmark, during the day, in some experiments no scavenging activity was recorded. Finally, scavenging behaviour also showed variations between the different habitat types. The most active habitat was the primary forest, and, in contrast, the least active habitat was the field edges. In additions, the level of scavenging was higher at night than during the day. Again, the results were not as expected, although the forest environment showed the strongest scavenging behaviour as initially thought, compared to other habitat types, the scavenging levels in the other habitats were much lower than expected. These results are different from our those on Terceira and some previously cited studies, including Sattler et al., (2010) that claims that

urban areas are home to a higher diversity of arthropod species. Our results suggested the opposite. It was also possible to differentiate between two types of habitats: wheat fields, field edges and urban areas and less anthropic habitats such as the primary forest. Here again, the habitat type influenced the scavenging behaviour. Habitats with less human activity had the highest level of scavenging and the highest number of species observed accidentally. This difference may be related to the fact that the habitats tested, such as fields or edge field, were the site of more intensive human activity. These agricultural activities could strongly impact arthropod populations. On the other hand, in the forest environment, arthropod species seemed to benefit from this less disturbed habitat. This means that the structure of this habitat, with its more open environment, with dead wood and litter, can offer a wide variety of shelters that can maintain scavenging arthropod species.

Comparison between Denmark and Terceira

The comparison between forest and urban habitats in Denmark and Terceira means that scavenger levels were also influenced by factors intrinsic to the habitats themselves. In other words, habitat composition had a strong influence on arthropod communities and their behaviour (Alvarado-Montero et al., 2021). Again, in the case of forests the difference between the two was conceivable as the environments were not similar. The native forest of Terceira is characterised by a weak community of necrophagous arthropods that relies mainly on slugs and snails according to our results, which is certainly a consequence of its geographical isolation. The primary forest in Denmark, is very active, has a higher level of activity and has a larger and more diverse community of scavenging arthropods. As far as urban areas are concerned, although structured in an equivalent way, there are significant differences in scavenging levels between the two territories. This means that factors other than the structure of the habitat and the day-night cycle come into play to explain these differences. It is very reasonable to think that climate has a major influence that could partly explain these differences. Further studies should be carried out on this subject.

Day-Night Cycle

Scavenging levels were strongly influenced by the day-night cycle. A habitat with scavenging activity during the day had greater or equal scavenging activity at night. However, this seemed to be corroborated by direct observations during the checks where on average one and a half to two times more species were incidentally observed in Denmark and Terceira. Our results seemed to indicate that the density and activity of scavenging invertebrates is

higher at night which may explain the difference in scavenging behaviour between day and night. The biggest difference (35-40%) between scavenging during the day vs. at night was registered in urban areas. One hypothesis that may explain this increase is that the urban area measurements were made on university campuses and that at night there was less human activity compared to daytime, which may inhibit or modify arthropod behaviour. However, we have no data to confirm or deny this assumption.

The rate of scavenging by arthropods

Scavenging is a low-risk way to obtain a highly nutritious resource, and invertebrates are very abundant in terrestrial ecosystems. Their populations renew themselves at a rapid rate, indicating that invertebrate carrion inputs alone are a very valuable biomass source (Alvarado-Montero et al., 2021). A range of organisms therefore have an interest in exploiting this resource. Microorganisms (bacteria, fungi) are widely distributed in the environment and have the advantage of being able to arrive to carcasses more quickly than scavenging arthropods. They have toxin production which is related to carcass colonisation and monopolisation (DeVault et al., 2003), but this takes some days. Thus, there is a window of opportunity during which scavenging arthropods can exploit the resource without risk of running into competition with microbes. They thus have access to an abundant and stoichiometrically more efficient resource than if they had to draw their energy from a lower trophic level. This also means that the energy captured at higher trophic levels is kept at that level, avoiding that some of that is lost due to higher conversion inefficiencies.

The identity of scavengers

Overall, apart from the beetles that were observed only in Denmark, the scavenging arthropods were quite similar between the two territories. Unfortunately, with the method we used we were not able to determine scientifically which group exactly was the main cause of the disappearance of the larvae. However, through occasional observations, we could see that ants were overwhelmingly present. Indeed, in Terceira, ants were present on 62% of our surveys and in Denmark it was 74%. Even if this observation was accidental, it allowed us to consider Formicidae as one of the main group responsible for the scavenging behaviour. The information gathered in the field seems to be in line with several studies that consider ants as one of the main scavenging arthropods (Eubanks et al., 2019; Holway & Cameron, 2021). Moreover, when ants were present, the scavenging dynamics were stronger. This is notably the case in the vineyards of Terceira, where ants represented 98.6% of arthropod observations. This translates into a high scavenging rate and a faster scavenging dynamic.

This is 1.2 times faster than the orchard and urban habitats where the proportion of ants observed was respectively 87.7% and 80.8%. While in the forest, no ant was observed, and the scavenging dynamics was 3 times slower. Conversely, although ants remain the dominant scavenger arthropod, this trend is weaker in Denmark, in the forest habitat, ants represented only 56.3% of observations and were not observed in the wheat fields, where beetles seemed to be more active, they represented 61.2% of observations. In addition, ants were observed in urban areas without impacting on scavenging levels which were very low. More studies need to be done on this subject to be able to draw clear conclusions. The prominence of ants also underlines the unequal contribution of various groups to any ecological function. In most single situations, only a fraction of biodiversity is responsible for most of the impact. However, this fraction is rarely identical in space and time (Isbell et al., 2015). Ants could well be an exception; they form an important group wherever they occur (D. & Goetsch, 1990)

The limitation of the method

The chosen method was an easy and cheap way to collect data on scavenging levels in different types of habitats. However, by choosing days without rain to standardise the method, we had to exclude some scavenging arthropods. In addition, we did not set up traps to collect and identify arthropods in order to get a clear idea of who is responsible for scavenging levels in different environments.

In conclusion

On the one hand, the levels of scavenging are higher than previously thought, with the rate of scavenging and its dynamics operating over a few hours in general. In view of these results, it is possible to consider arthropod scavenging as an ES that operates at a relatively high level. In anthropic environments it is certainly a basic ES that has its limits as shown by Denmark and its low levels of scavenging in anthropized environments.

On the other hand, the influence of scavenging arthropods on arthropods is certainly underestimated which contributes to a limited understanding of the food web and nutrient cycling. As for example in the native forest of Terceira, scavenging behaviour seems to be different from that in anthropic environments. Food web dynamics seem to be less dependent

on resource acquisition through scavenging and nutrient cycling seems less dependent on arthropod scavenging.

Furthermore, there are significant differences between the different types of habitats within each territory and between habitats within different territories. The structure of the habitats influences the arthropod community and therefore the scavenging behaviour. The day-night cycle also influences scavenging behaviour, although it is always higher or equal during the night. Finally, there are other factors that influence the level of scavenging, and further studies are needed to determine these.

It would be important to preserve or increase the levels of arthropod scavenging, which can be beneficial in many ways for human activities (soil structure, nutrient redistribution, biodiversity). Thus, finding a way to increase and maintain this ES could have useful implications for agriculture.

Annexes

Tables

Table 1 Coordinates of the sites used for this experiment in Terceira, Azores, Portugal.

Habitat	Site	Coordinates (latitude & longitude)
Native forests	Jungle_cross	38.747414 -27.198759
	Stoneage	38.745325 -27.198243
	Matela	38.745325 -27.198243
	Cedrorum	38.699495 -27.259701
Orchards	St Bartolomeu coriander	38.669922 -27.241139
	St Bartolomeu control	38.669922 -27.241139
	Bica coriander	38.680613, -27.275742
	Bica control	38.680853, -27.275897
Vineyards	Simas control	38.796424, -27.256487
	Simas coriander	38.797016, -27.256212
	Coop GR 1	38.796025, -27.264076
	Coop GR 2	38.796259, -27.262726
Urban area	site 1	38.659065, -27.232084
	site 2	38.658795, -27.233498
	site 3	38.658223, -27.233346
	site 4	38.658517, -27.234789

Table 2 Coordinates of the sites used for this experiment in Flakkebjerg, Zealand, Denmark.

Habitat	Site	Coordinates (latitude & longitude)
Sorø Forest	Sorø 1	55.378486 , 11.566446
	Sorø 2	55.378428, 11.564835
	Sorø 3	55.378292, 11.564348
	Sorø 4	55.378674, 11.565274
	Site 1	55.324718, 11.386774

Field	Site 2	55.324857, 11.386111
	Site 3	55.325035, 11.385982
	Site 4	55.324876, 11.386631
Field edge	Site 1	55.322522, 11.385412
	Site 2	55.321016, 11.386223
	Site 3	55.322478, 11.414045
	Site 4	55.322846, 11.414511
Urban area	Site 1	55.325884, 11.390910
	Site 2	55.326400, 11.391251
	Site 3	55.325831, 11.390279
	Site 4	55.325814, 11.389151

Pilot tests

Pilot experiment 1: Test the type of glue.

The experiment took place at the University of the Azores, Terceira, Portugal, between 24/03/2021 and 26/03/2021. It consisted of placing 15 cards with 25 *Drosophila* carcasses glued with three different glue types (5 replicates per treatment).

The gluing methods tested were: flour glue (water+flour), "Supertite" white glue, and "Bangi" double-sided tape.

A drop of glue was applied to the cards using the end of a toothpick. For the double-sided tape, 4mm squares were placed on the cards.

The cards were held face down 2-3cm above the ground supported by two toothpicks placed at two diagonally opposed corners. The cards were placed soils with and without vegetation. Soils without vegetation were prepared by manually removing grasses and other plants.

Results

Terceira, Portugal

Soils with no vegetation favour rate (mean=70.6%, sd= 33.3%, n=15) compared to soils

with vegetation (mean=52.8%, sd= 43%, n=15).

The overall scavenging rate were 58.4% (sd= 46.4%, n=15) for white glue, 76.8% (s.d.= 25%, n=15) for flour glue, and 44.8% (sd= 45.7%, n=15) for the double-sided tape. A Tukey test suggests that there was no difference between the scavenging rates on the different types of glue used during these trials.

Conclusion

To reduced biases, we selected white glue and decided to work with soils with no vegetation, i.e., standardisable by clearing a small area of 4 to 5 cm on each side when placing the cards.

Pilot experiment 2: Exposure time

In accordance with the literature (Tolonen, 1995), we exposed cards for 48h in different orchards, where 3 to 6 sites per habitat were selected and tested (Table 1).

Results

All cards were completely emptied of all larvae. However, sometimes it was possible to observe parts of the cuticle. Scavenging rates after 48h was 100% at all sites except for Bica (orchard). Some cards, particularly those in the orchards, showed traces of small mammal teeth (rats or mice). The experiment was repeated with 24h exposure time but scavenging rates was 100% everywhere.

Pilot experiment 3: Exclusion of mammals.

In agreement with the field observations, we wanted to exclude small mammals from our experiments. To do this, we created cages using clear plastic Tupperware, and taping a 1 x 1 cm net to allow arthropods but not small mammals to access the cards. (See Materials and Methods, Mammal Exclusion section)

Results

No significant difference between the cards could be observed. Moreover, the scavenging rates were always 100%.

Conclusion

Small mammals did not have a significant influence on the previous results. Arthropods removed all the carcasses from the cards in 24h or less.

Pilot experiment 4: Time

To ensure that the high scavenging rates observed were not due to the high density of larvae on the cards (25), we reduced this number to 10 larvae per card. On 12/05/21, we placed 5 cards in 4 sites in two orchards and recorded scavenging rates every 2h between 09:30 and 12:30 in San Bartolomeu and 09:45 and 12:45 in Bica. The cards were spaced more or less 5m apart.

Results

The final scavenging rates were 63% % (sd= 43.1%, n=4) in San Bartolomeu and 16.7% (sd= 40.8%, n=4) in Bica .

Conclusion:

It seems relevant to monitor the evolution of the scavenging rate over time over relatively short periods in order to highlight its variation according to the habitats.

Conclusion of the pilot tests

Following the pilot experiments, we decided to measure scavenging rates every 2 hours over a period of 10 hours.

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