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DISTRIBUTION AND HABITAT PREFERENCES OF THE HAZEL DORMOUSE IN THE SWISS VALLEY OF VAL-DE-RUZ AS A FUNCTION OF VEGETATION AND THE LANDSCAPE CONTEXT

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A young hazel dormouse encountered above Valangin (photograph by Clément Vaudroz).

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Abstract

The hazel dormouse (HD) is classified as vulnerable (VU) in Switzerland, but the actual status of the Swiss population as well as its ecological habits are poorly known. Yet, the presence of the species is indicative of the health and quality of the natural environments to which it is found, mostly, shrub-rich woody environments. Therefore, there is a clear interest in knowing more about the species, because the evolution of its populations can serve as a proxy for evaluating the effectiveness of measures taken to protect, revitalise or even recreate natural habitats.

In this respect, the Val-de-Ruz is a perfect context to study HD populations. The region consists of a patchwork of agricultural, urban, natural, and semi-natural areas crisscrossed by multiple vegetated structures. The first objective of this work was to improve knowledge of the distribution of the HD in the agricultural zone of Val-de-Ruz, over a representative sample of woody patches. Then, the composition and structural properties of the vegetation of the studied transects were measured to establish which local habitat factors are better related to the presence of the HD. All selected transects were part of a regional *ecological network*. Thus, the proportion of neighbouring areas inventoried as ecological corridors was also assessed for its potential effects on the presence of the species. Finally, the municipality of Val-de-Ruz switches off its public lighting between 00:00 and 04:45. Therefore, the distance from sources of light pollution was studied as another potential explanatory variable for the presence of the HD.

Data regarding the presence of HD were collected using the footprint tunnel method, complemented by searching for HD nests. The results confirmed the establishment of the HD in the agricultural zone of Val-de-Ruz but suggest that it struggles to spread throughout the *ecological network*. The data also support that the HD prefers well-developed shrub layers and diversified tree layers and that landscape management practices could be improved. Light pollution indices were considered indistinguishable from overall urban disturbances but confirmed that the HD partly avoid populated areas. Our results underline the relevance of further long-term conservation projects for HD in the Val-de-Ruz.

Keywords : hazel dormouse (HD), footprint tunnels, ecological network, light pollution.

Résumé

Le Muscardin est classé vulnérable (VU) en Suisse, mais le statut réel de sa population, ainsi que ses habitudes écologiques sont mal connus. Pourtant, la présence de l'espèce est indicatrice de la santé et de la qualité des milieux naturels dans lesquels elle vit, soit principalement les milieux boisés riches en arbustes. Il y a donc un intérêt certain à mieux connaître l'espèce, car l'évolution de ses populations peut servir de proxy pour évaluer l'efficacité des mesures prises pour protéger, revitaliser ou même recréer des habitats naturels.

À cet égard, le Val-de-Ruz est un contexte idéal pour étudier la population de Muscardin. La région se compose d'une mosaïque de zones agricoles, urbaines, naturelles et semi-naturelles traversées par de nombreuses structures végétalisées. Le but premier de ce travail était d'améliorer les connaissances sur la distribution de ce gliridé dans la zone agricole du Val-de-Ruz, à partir d'un échantillon représentatif de structures paysagères boisées. Ensuite, la composition de la végétation et les propriétés structurelles des transects étudiés ont été mesurées afin d'établir quels facteurs de l'habitat local étaient majoritairement reliés à la présence du Muscardin. Tous les transects sélectionnés font partie d'un réseau écologique régional. Ainsi, la proportion de zones voisines inventoriées en tant que Corridor Écologique a également été évaluée pour ses effets potentiels sur la présence de l'espèce. Enfin, la commune de Val-de-Ruz éteint son éclairage public entre 00h00 et 04h45. La distance aux sources de pollution lumineuse a donc été étudiée comme une autre variable potentiellement explicative de la présence des Muscardins.

Les données de présence du Muscardin ont été collectées à l'aide de la méthode des Tunnels à Traces, complétée par la recherche des nids de l'espèce. Les résultats confirment l'établissement du Muscardin dans la zone agricole du Val-de-Ruz, mais suggèrent qu'il peine à se disperser au travers du réseau écologique. Les données confirment également que les spécimens étudiés préfèrent les couches arbustives

bien développées, ainsi que les strates arborées diversifiées, et que les pratiques de gestion du paysage pourraient être améliorées. Les indices de pollution lumineuse ont été considérés comme indiscernables de l'ensemble des perturbations urbaines, mais ont confirmé que le Muscardin évite en partie les zones peuplées. Nos résultats soulignent la pertinence de mettre en place de nouveaux projets pour la conservation à long terme du Muscardin dans le Val-de-Ruz.

Mots clés : Muscardin, tunnels à traces, réseaux écologiques, pollution lumineuse.

Zusammenfassung

Die Haselmaus ist in der Schweiz als gefährdet (VU) eingestuft, aber der tatsächliche Status der Schweizer Population sowie ihre ökologischen Gewohnheiten sind schlecht bekannt. Das Vorhandensein der Art ist ein Indikator für den Zustand und die Qualität der natürlichen Umgebung, in der sie sich aufhält, vor allem in buschreichen Wäldern. Es besteht ein Interesse, mehr über die Art zu erfahren, da die Entwicklung ihrer Populationen als Indikator für die Wirksamkeit von Massnahmen zum Schutz, zur Revitalisierung oder sogar zur Wiederherstellung natürlicher Lebensräume dienen kann.

In dieser Hinsicht ist das Val-de-Ruz ein ideales Umfeld für die Untersuchung von Haselmauspopulationen. Die Region besteht aus einem Mosaik aus landwirtschaftlichen, städtischen, natürlichen und halbnatürlichen Gebieten, die von zahlreichen Vegetationsstrukturen durchzogen sind. Das erste Ziel dieser Arbeit bestand darin, die Kenntnisse über die Verbreitung der Haselmaus in der landwirtschaftlichen Zone des Val-de-Ruz mittels in einer repräsentativen Auswahl von bewaldeten Flächen zu verbessern. Anschliessend wurden die Vegetationszusammensetzung und die strukturellen Eigenschaften der untersuchten Transekte gemessen, um festzustellen, welche lokalen Lebensraumfaktoren am besten mit dem Vorkommen von Haselmäusen zusammenhängen. Alle ausgewählten Transekte waren Teil eines regionalen ökologischen Netzwerks. Daher wurde auch der Anteil der benachbarten Gebiete, die als ökologischer Korridor inventarisiert wurden, auf seine möglichen Auswirkungen auf das Vorkommen der Art untersucht. Schliesslich schaltet die Gemeinde Val-de-Ruz ihre öffentliche Beleuchtung zwischen 00:00 und 04:45 Uhr aus. Die Entfernung zu Quellen der Lichtverschmutzung wurde daher als weitere potenzielle Erklärungsvariable für das Vorkommen von Haselmäusen untersucht.

Die Daten über das Vorkommen der Haselmaus wurden mit der Methode der Fussspurentunnel gesammelt, ergänzt durch die Suche nach Nestern der Art. Die Ergebnisse bestätigen die Ansiedlung der Haselmaus in der Landwirtschaftszone des Val-de-Ruz, deuten aber darauf hin, dass die Haselmaus Schwierigkeiten hat, sich im gesamten Ökologischen Netzwerk auszubreiten. Die Daten belegen auch, dass die untersuchten Exemplare gut entwickelte Strauchschichten und abwechslungsreiche Baumschichten bevorzugten und dass die Landschaftspflege verbessert werden könnte. Die Auswirkung der Lichtverschmutzung ist nicht unterscheidbar von den allgemeinen städtischen Störungen, aber es konnte bestätigt werden, dass Haselmäuse besiedelte Gebiete teilweise meiden. Unsere Ergebnisse unterstreichen die Bedeutung weiterer langfristiger Schutzprojekte für Haselmäuse im Val-de-Ruz.

Stichwörter : Haselmaus, Fußabdrücken Tunnel, Ökologischer Verbund, Lichtverschmutzung.

INTRODUCTION

The hazel dormouse (HD), *Muscardinus avellanarius* L. (Gliridae, Rodentia) and its habitats are protected by *The Federal Act on the Protection of Nature and Cultural Heritage*. However, knowledge about the Swiss population is very weak and incomplete compared with some other micromammals (e.g., *Apodemus* spp.) (CAPT, 2022; HAAG, 2014; JUŠKAITIS, 2008; MARCHESI *et al.*, 2011). This situation is largely due to the poor effort in monitoring and safeguarding the species in Switzerland: there have been only two low-range studies in the past decade (BLANT, 2015; HAAG, 2014). Most data are from opportunistic encounters recorded by private or birdwatching associations, often in nest boxes. Thus, there have not been enough detections to assess the decline of the species populations and to assign a reliable degree of threat. The HD has been classified as vulnerable (VU), mostly based on the decline of its assumed environments, rather than on an actual population reduction (CAPT, 2022; HAAG, 2014; INFO FAUNA [CSCF & KARCH] & CCO-KOF, 2022a; WEINBERGER & BRINER, 2022). Therefore, there is currently a great need for more systematic surveys to better assess the status of HD populations in Switzerland, as well as their ecological habits.

Indeed, the HD may become a “key species” for the conservation of woody habitats. Although glirids can be found in a wide variety of vegetated habitats, they must have a specific combination of ecological properties to meet the species’ strict requirements (HITCHCOCK, 2019). First, the HD relies on higher levels of plant diversity in its habitat (HAAG, 2014; JUŠKAITIS, 2008; MORTENSEN *et al.*, 2022). The species is generally active from early spring to mid-autumn (late March/early April to mid-November) depending on the country. A greater diversity of plants can provide buds, flowers, fruits, or insects, ensuring an uninterrupted sequence of food availability throughout the HD’s period of

activity (BRIGHT *et al.*, 2006; FEDYŃ *et al.*, 2021; GOODWIN *et al.*, 2020; JUŠKAITIS, 2008; MORTENSEN *et al.*, 2022; RAMAKERS *et al.*, 2014a). Second, the HD is highly dependent on the structure of its habitats: it lives in dense and ramified shrubby layers that are in continuity with tree and herbaceous strata; these features facilitate its movements (BRIGHT *et al.*, 2006; HAAG, 2014; JUŠKAITIS, 2008; MORTENSEN *et al.*, 2022; TESTER, 2018; WHITE & HUNT, n.d.). Third, the HD relies on the connectivity between the patches of woody habitats for its dispersion at the landscape scale. Habitat fragmentation and the resulting isolation of populations can lead to local extinctions (BRIGHT *et al.*, 2006; DIETZ *et al.*, 2018a; HAAG, 2014; JUŠKAITIS, 2008; MORTENSEN *et al.*, 2022).

The HD is both an *indicator species* and an *umbrella species* for the traditional extensive agriculture of British bocages, which typically consist of a mosaic of crops interspersed with hedgerows and punctuated by woodland patches. As the only native member of Gliridae in the UK, over the past 20 years, the HD has become a *flagship species* in the fight to safeguard these semi-natural landscapes (AL-FULAIJ *et al.*, 2018; BRIGHT *et al.*, 2006).

The region of Val-de-Ruz in the Swiss canton of Neuchâtel is one of the few agricultural areas of the country that is still partially covered by semi-natural woody structures that are characteristic of British, but more widely of European extensive farming practices (BENZ *et al.*, 2015, 2021; LUGON & BILAT, 2004). In Val-de-Ruz, many wooded structures constitute *natural corridors*, that is, a set of objects and patches of natural environments (also aquatic or mountain habitats, etc.) that are more or less close to one another and that are maintained or safeguarded by humans to enable biodiversity to disperse through landscapes often fragmented by anthropic activities. An interconnected whole of multiple *natural corridors* designed and

maintained together constitute an *ecological network*. For almost two decades, biologists, local authorities, and farmers in Val-de-Ruz have cooperated to develop such a network (CAMPO, 2014; DIETZ *et al.*, 2018a; KOLLER *et al.*, 2020; LUGON & BILAT, 2004; LUGON & JACOT-DESCOMBES, 2008; RÉPUBLIQUE DU CANTON DE NEUCHÂTEL, 2004; SORDELLO, 2017; SORDELLO *et al.*, 2021; VONLANTHEN & RAMSEIER, 2009).

While researchers have found that linear woody structures are ideal for the HD to live and disperse (CAPT, 2022; DIETZ *et al.*, 2018b; EHLERS, 2012; JUŠKAITIS, 2008; TESTER, 2018), that most vital plant species to the HD vary across studies and regions, possibly because of its foraging plasticity or differences across populations throughout Europe (RAMAKERS *et al.*, 2014a). Identifying the specific needs of the local HD populations in Val-de-Ruz could help any conservation project refine its objectives (FEDYŃ *et al.*, 2021).

Besides being an indicator of human disturbance to vegetation and landscapes, the HD could help evaluate the consequences of other types of nuisances (BRIGHT *et al.*, 2006; DIETZ *et al.*, 2018a; HAAG, 2014; JUŠKAITIS, 2008; WHITE & HUNT, n.d.). Light pollution is now a major environmental issue whose awareness has increased in recent decades, as the magnitude of the phenomenon continues to grow. In Switzerland, skyward light emissions have almost doubled between 1994 and 2020 (GASTON *et al.*, 2013; LARGE NETWORK GENÈVE *et al.*, 2022; OFFICE FÉDÉRAL DE L'ENVIRONNEMENT [OFEV], 2021; RANZONI *et al.*, 2019). Yet around 30% of the vertebrates and 65% of the invertebrates are nocturnal and potentially affected by light pollution (SORDELLO *et al.*, 2014, 2021). The harmfulness of light to organisms depends on many physical factors. The physiological impact for each taxon is different, so the same light conditions can be detrimental to some species while beneficial to others (GASTON *et al.*, 2013; OFEV, 2021; SORDELLO *et al.*, 2021).

For each type of habitat (forests, rivers, lakes, grasslands, etc.), we must identify *model species* whose requirements encompass those of most species in their ecosystem (SORDELLO *et al.*, 2014, 2021). Although a lot of data have already been collected on bats, only a few papers have been published about other mammalian taxa (BEIER *et al.*, 2013; SORDELLO, 2017; SORDELLO *et al.*, 2014). Nocturnal micromammals (Rodentia and Eulipotyphla) are especially poorly studied, but a few existing studies support that these taxa are also negatively affected by light pollution (BEIER *et al.*, 2013). The HD could constitute an indicator species for micromammals in general as it is potentially very sensitive to this type of nuisance. As evidenced by its large black eyes, the species has strong nocturnal habits. Its torpor-activity rhythms, characteristic of Gliridae, are deeply linked to seasonal variations in day–night duration (BEIER *et al.*, 2013; BRIGHT *et al.*, 2006; DIETZ *et al.*, 2018a; HAAG, 2014; JUŠKAITIS, 2008; SORDELLO *et al.*, 2021; WHITE & HUNT, n.d.). The HD could also help to understand how light pollution affects the quality and the fragmentation of woodland habitats (BEIER *et al.*, 2013; BRIGHT *et al.*, 2006; DIETZ *et al.*, 2018a; HAAG, 2014; JUŠKAITIS, 2008; SORDELLO, 2017; SORDELLO *et al.*, 2014, 2021; White & Hunt, n.d.).

We attempted an exploratory approach to account for the light pollution effects on the distribution and ecological requirements of the HD population in Val-de-Ruz. However, night pictures of the region suggest that even though midnight extinction visibly reduces the “Halo effect” above the valley (i.e., dome-like diffusion of the light above urban areas due to refraction by the atmospheric particles), much light is constantly emitted towards the horizon by buildings (homes, businesses, etc.), which could be the main sources of light pollution (OFEV, 2021; SORDELLO *et al.*, 2014, 2021). Indeed, these buildings could provide much more light pollution than streetlamps, whose location is correlated with the distribution of

residential areas (JURA TROIS-LAC PAYS DE NEUCHÂTEL, 2022).

In Switzerland, footprint tunnels are recommended by the *Swiss Red List of Terrestrial Mammals* to monitor glirids (CAPT, 2022). In the present work, we attempted to use exclusively and on a larger scale aseptic carton footprint tunnels rather than the traditional larger plywood tunnels (HAAG, 2014). Besides, we completed the tunnel survey by searching for the HD's summer nests (BRIGHT *et al.*, 2006; BULLION *et al.*, 2018).

This study comprised three aims. Our first aim was to determine the state of the HD distribution in the agricultural areas of Val-de-Ruz. Based on the composition and size of the collected HD nests, we also tried to determine the potential extent of its breeding. Given the specific ecological requirements attributed to the species, only woody structures with adequate properties should host the HD. Our second aim was to investigate the type of patches, the plant composition, and the structural characteristics that best predict the presence of the HD. We hypothesise that transects with more structured and diversified shrub layers are most occupied by the HD (AL-FULAIJ *et al.*, 2018; BRIGHT *et al.*, 2006; BULLION *et al.*, 2018; HAAG, 2014). Because the HD is assumed to be an indicator of good connectivity between habitats, its distribution could also reflect the fragmenting effects of light pollution (BEIER *et al.*, 2013; BRIGHT *et al.*, 2006; HAAG, 2014; SORDELLO *et al.*, 2014). Our third aim was to examine whether the proportions of light pollution sources or areas listed in the *ecological network* influence the presence of the HD. We hypothesise that there is greater presence data obtained closest to other structures related to the Val-de-Ruz's *ecological network*, but more distant from light pollution (DIETZ *et al.*, 2018a).

MATERIALS & METHODS

The survey area

Situated in a syncline of the Jura Arc, Val-de-Ruz is a mosaic of urbanised areas, intensive and extensive agricultural areas, and patches of natural and semi-natural environments. For almost two decades, a wide *ecological network* has been put in place and continues to expand. The valley is surrounded by forest and dotted with various woody habitats. It is crisscrossed by numerous hedgerows in its extreme west and by many streams with vegetated banks throughout the rest of its area. These various watercourses all flow into a main arteria, the Seyon, which crosses Val-de-Ruz from northeast to southwest. The Seyon and its numerous tributaries, mostly drainage pipes, form a substantial part of the Val-de-Ruz *ecological network* (SWISS CONFEDERATION, 2022). Nevertheless, a large and growing part of the network consists of agricultural areas reserved for promoting biodiversity, mostly extensive meadows with high floral quality, as well as grassy strips at the margins of the crops, which run along woody habitat patches (LUGON & BILAT, 2004). While Swiss farmers receive subsidies to create, manage, and maintain areas reserved for promoting biodiversity, extra subsidies are granted by the *Neuchâtel Cantonal Agricultural Service* when landowners agree to comply with the additional requirements associated with the networking project (RÉPUBLIQUE DU CANTON DE NEUCHÂTEL, 2004).

On 14 August 2020, the commune of Val-de-Ruz became the largest in Switzerland to switch off all its public lighting overnight, that is, between 00:00 and 04:45. In addition to the goals of saving energy and public money as well as improving the population's well-being, this project aimed to reduce the impacts of light pollution on the environment (BONVIN *et al.*, 2020).

Aseptic carton footprint tunnels

Footprint tunnels are tube-like structures with an inner platform with one or more inking pads alongside sheets of paper. When an animal passes through the tunnel, its paws become impregnated with ink and are its pawprints are printed on the sheets of paper. In this respect, footprint tunnels are an indirect and non-invasive method, as it does not require capturing or manipulating individuals (CAPT, 2022; CAPT *et al.*, 2014; HAAG, 2014). Similarly, the device does not require any bait and relies on the curiosity of the animals (BULLION *et al.*, 2018; HAAG, 2014; HITCHCOCK, 2019). In addition to these advantages, footprint tunnels have low complexity and a low cost in terms of time and money (CAPT *et al.*, 2014).

The *Swiss Red List of Terrestrial Mammals* protocol recommends using plywood tunnels whose dimensions (1 m long, 18.5 cm high, and 14.5 cm wide) and weight (4.5 kg) make them cumbersome (CAPT, 2022). These tunnels are used to survey many tree and ground-related taxa, such as mustelids, rodents, and members of Eulipotyphla. However, they are unnecessarily big when the target species being monitored are such small as glirids. Overall, footprint tunnels are particularly suitable for monitoring the HD, as the footprints of this species are easily distinguished from those of other mammals of a similar size. The HD footprint presents typical triangle-shaped marks printed by their planar pads (fig. 1) (HAAG, 2014; MARCHESI *et al.*, 2011; MELCORE *et al.*, 2020a, 2020b).

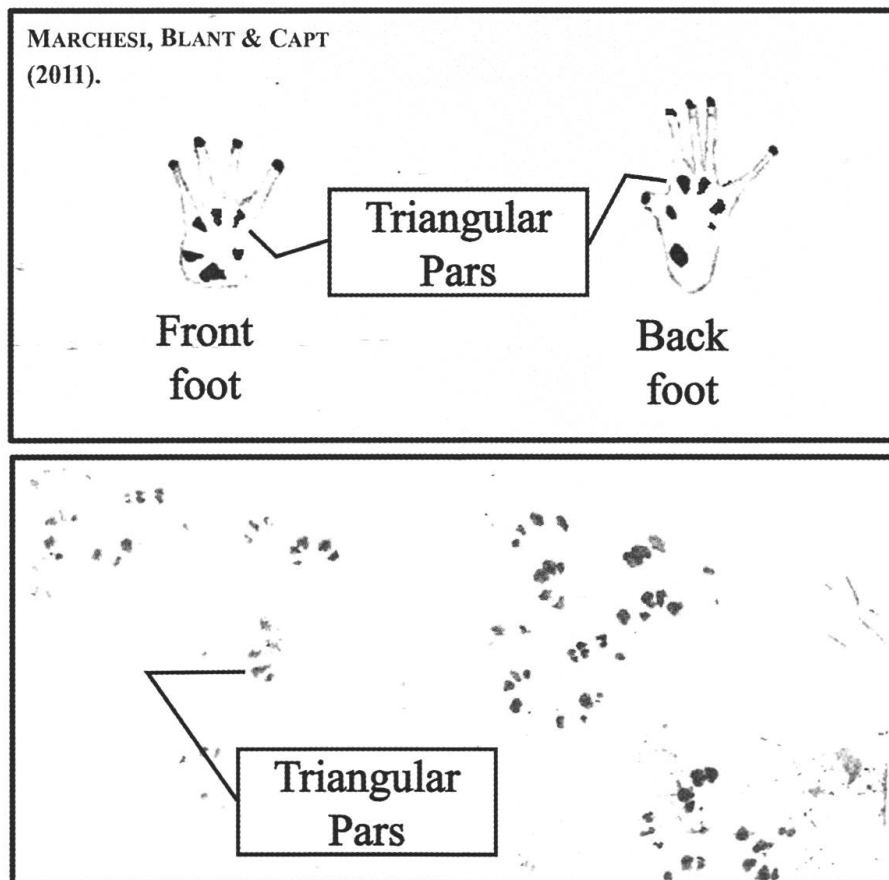


Figure 1. Footprints of the hazel dormouse.

To facilitate HD surveys, HAAG (2014) conceptualised a new type of footprint tunnel built with aseptic cartons (i.e., Tetra Pak®), which is generally considered poorly recyclable waste. Aseptic carton footprint tunnels are much less expensive and lighter (~ 65 g.) than plywood footprint tunnels. They also significantly reduce the field workload because they are easier to carry, fix in trees, check, and reload (BULLION *et al.*, 2018; HAAG, 2014; MÄLDIG, 2014; MARCHESI *et al.*, 2011). These arguments convinced us to draw on the methodology of HAAG (2014).

For the present survey, pharmaceutical-grade activated charcoal and grape seed oil were mixed in a 1:5 ratio (w/v) to create the ink. The ink pads were cut systematically from old but clean dusters (80% polyester and 20% polyamide). Cardstock was used instead of regular copy paper as the pre-tests highlighted the former better absorbs ink, increases rain resistance (e.g., preserving tracks even after soaking and drying), and improves footprint readability thanks to its greater whiteness.

The aseptic carton footprint tunnels were built according to the methods recommended by the Swiss dormouse conservation association Pro Bliche, which is based in Basel. A few improvements were introduced to increase water resistance. In particular, the tongues were stapled to the platforms towards the rear to avoid the formation of gutters likely to retain water (BULLION *et al.*, 2018; CHÈVRE *et al.*, 2022; HAAG, 2014; HAAG & TESTER, 2014; MÄLDIG, 2014; TESTER, 2018).

Aseptic carton footprint tunnels were fixed on horizontal branches at about 1–1.5 m above the ground level – the stratum that the HD prefers (HAAG, 2014; OPENGIS.CH GMBH, 2022; RAMAKERS *et al.*, 2014a). The tunnels were controlled every (\pm) 7 days (BULLION *et al.*, 2018; HAAG, 2014; HITCHCOCK, 2019; MELCORE *et al.*, 2020a). The tunnel survey was conducted over 10 weeks between 16 July and 16 September (HAAG, 2014).

Potential footprint marks were assessed using essentially the reference book *Mammals of Switzerland – Identification Keys* together with additional criteria found in the literature (BLANT, 2015; BLANT *et al.*, 2012; BULLION *et al.*, 2018; CAPT *et al.*, 2014; MARCHESI *et al.*, 2011). Footprints of the garden dormouse (*Eliomys quercinus*) and the edible dormouse (*Glis glis*) were also examined, but they were not expected to be found because they were not targeted by the methods and are less present in Val-de-Ruz (CAPT, 2022; FEDYŃ *et al.*, 2021; INFO FAUNA [CSCF & KARCH] & CCO-KOF, 2022b; JUŠKAITIS, 2008; MELCORE *et al.*, 2020a; RÉDACTION WEB *et al.*, 2022; WEINBERGER & BRINER, 2022). Besides, many footprints were left by other non-Gliridae micromammals, especially voles and wood mice. Still, their footprints are very similar in size and shape and can also vary according to the age of the individuals and unintentional factors such as the positioning of the platform or the type of paper. Therefore, footprints that were particularly hard to identify, even for specialists, were recorded as “unidentified rodents” (BLANT, 2015; BLANT & ERNE, 2020; BRIGHT *et al.*, 2006; CAPT *et al.*, 2014; MARCHESI *et al.*, 2011; MELCORE *et al.*, 2020b).

The information obtained from footprint tunnel surveys cannot be treated as iterative presence/absence data used in traditional occupancy models. Indeed, the HD is a sedentary species: it builds a nest for reproduction as well as sleep. This means that as soon as footprints are recorded at a surveyed site, the probability of detection at that site can no longer be assumed to be equal to that at other sites. Similarly, the dispersal of young HD in the autumn and their potential permanent settlement at their arrival site means that the occupancy state is unclosed and the detectability is uneven (BAILEY & ADAMS, 2005; BRIGHT *et al.*, 2006; BULLION *et al.*, 2018; JUŠKAITIS, 2008; MACKENZIE, 2005). Thus, the detection data from the footprint tunnel survey were condensed in time and compiled as a single shot presence/absence information (BAILEY & ADAMS, 2005; BULLION *et al.*, 2018).

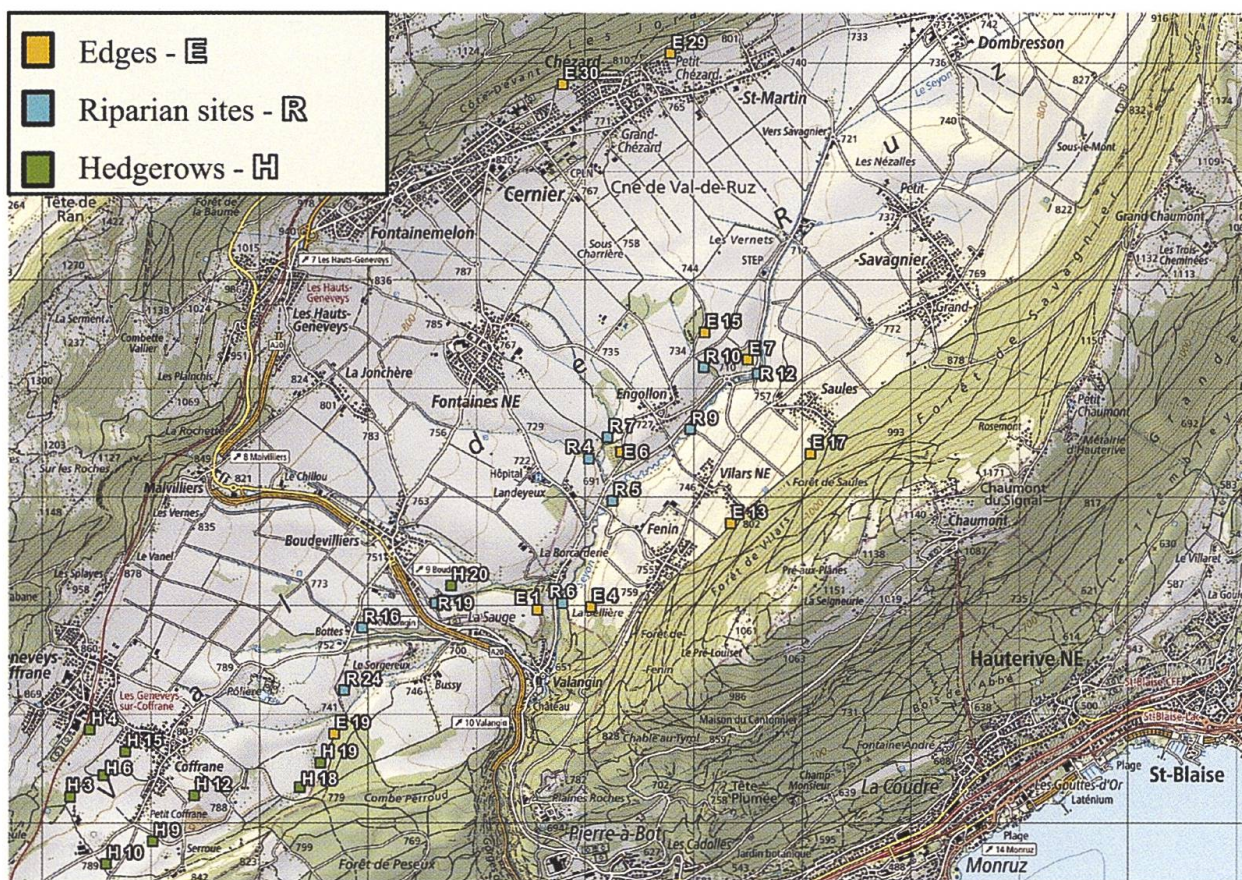


Figure 2. Location and structure type of the surveyed transects.

The transect design

The survey involved 30 transects of 100 m in length (fig. 2), with five tunnels each ($5 \times 30 = 150$ tunnels), interspaced by about 20 m depending on the vegetation (CAPT *et al.*, 2014; CHANIN & GUBERT, 2012; HAAG, 2014; RAMAKERS *et al.*, 2014a). Thus, three groups of 10 transects were selected based on the three main kinds of woody structures forming the *ecological network* of the Val-de-Ruz: hedgerows, edges, and riparian vegetation. Given the mean territory size of the HD is less than about 1 ha, the transects were spaced at least 100 m based on geographic information system (GIS) tools (BRIGHT *et al.*, 2006). Linear vegetation structures were considered as more or less abrupt transition between a patch of wooded vegetation and open areas. Structures were categorised

as described previously (LUGON & JACOT-DESCOMBES, 2008; HITCHCOCK, 2019; INFO FAUNA [CSCF & KARCH] & CCO-KOF, 2022a; RÉPUBLIQUE DU CANTON DE NEUCHÂTEL, 2004; SITN, 2022; SMIGAJ & GAULTON, 2021; SWISS CONFEDERATION, 2022):

Hedgerows (H) – any isolated line of vegetation greater than 2 m in width and distinct from any other linear structure;

Riparian vegetation (R) – any linear woody structure within the 100 m radius of a water stream;

Edges (E) – selected from among the boundaries of areas classified as forests from the *national ecological network* (REN) by the federal GIS data.

The 30 transects were subjectively selected according to their apparent suitability for the HD (for coordinates, see appendix 1), that is, their superficial plant diversity and their structural linear continuity. This screening was intended to increase the chances of detecting this rare species, whereas a strictly random selection of transects could have biased our sample towards unsuitable transects (BLANT, 2022).

Nest research

The size and arrangement of the HD summer nests constitute indices for actual reproduction. They are classified as breeding and simple sleeping nests. The breeding nests are bigger (>10 cm) than the sleeping ones (< 10 cm) and are built only by females during the reproductive period, from late spring to late summer. The sleeping nests are built by both sexes at all ages during the entire activity period (BRIGHT *et al.*, 2006; HAAG, 2014; JUŠKAITIS, 2008). In addition, nests are often classified into four other categories according to the type and arrangement of plant material they contain (JUŠKAITIS, 2008).

1. **Mixed nests (Mx)** – Tree or shrub leaves woven together with grass blades. The walls of these nests are made of a mixture of the two types of vegetal material.
2. **Layered nests (Ly)** – The nests are composed of two distinct layers. The outer layer is generally made from tree leaves. The inner layer is weaved with finer material (grass, fibre). Layered nests are typically considered breeding nests.
3. **Grassy nests (Gr)** – These nests consist of a dense sphere of dry grass blades and occasionally stems.
4. **Foliar nests (Fl)** – These nests are made of either fresh or dry tree or shrub leaves, although some grass material may also be used.

The above criteria served to identify transects where breeding events potentially occurred. The search for nests was conducted between 6 and 15 November (AL-FULAIJ *et al.*, 2018; BULLION *et al.*, 2018). To maximise success, the survey was systematically carried out by a pair of observers. Each transect was walked twice from one end to the other and the effort adapted to the vegetation density of the transects varied from 45 minutes to 2 hours, for a total survey time of 36 hours (BLANT *et al.*, 2012).

Nests were photographed as discovered on their plant support to link the position of the nests to structural vegetation variables. Thus, the nest discovery sites were recorded according to the vegetation context: the herbaceous layer (HL), the shrub layer (SL), or the tree layer (TL). The distinction between the SL and the TL was based on the same criteria as for the survey of ligneous plant diversity (see “Vegetation structural variables” below). Brambles were considered part of the herbaceous layer, as for most transects these formed vegetation mats rarely exceeding 50 cm (BERGAMINI *et al.*, 2020). Nests were searched in the first metre of vegetation and between 0 to 3 m above the ground, and sampled to avoid double counting (BLANT, 2015; BLANT *et al.*, 2012).

Vegetation structural variables

Inspired by RAMAKERS *et al.* (2014), Table 1 lists the variables that were recorded as descriptors for the structure of the vegetation in the transects (EHLERS, 2012; GOODWIN, SUGGITT *et al.*, 2018; RAMAKERS *et al.*, 2014a, 2014b; TESTER, 2018; VANNESTE *et al.*, 2020).

For the HTT and HTS indices, vegetation height was measured every 5 m using the Vertex 5 ® (HAGLÖF SWEDEN AB, 2021; VANNESTE *et al.*, 2020). An arithmetic mean of a maximum of 20 height measurements was derived (RAMAKERS *et al.*, 2014a, 2014b).

Table 1. List of vegetation structural variables.

Structural variable	Measurement method	Variable type	Scale
Mean height of the top trees layer (HTT)^a	Ultrasonic instrument Vertex 5 ® (Haglöf Sweden AB, 2021)	Continuous quantitative	[metre ± 0.1 m]
Mean height of the top shrubs layer (HTS)^b	Ultrasonic instrument Vertex 5 ® (Haglöf Sweden AB, 2021)	Continuous quantitative	[metre ± 0.1 m]
Horizontal structuring of the shrub layer (HS)	Naturalistic subjective assessment	Ordinal qualitative	6 levels [1–6] ^c
Coverage by the shrub layer (CS)	Naturalistic subjective assessment	Ordinal qualitative	6 levels [1–6] ^d
Structure type (Structure_type)	Naturalistic subjective assessment	Categorical nominal	Hedgerows (H) Edges (E) Riparian Vegetation (R)

^a Regardless of their size, all woody plants with trunks distinguishable from an upper crown with higher ramification level were classified as trees.

^b Regardless of their size, all woody plants with a high global level of ramification, making it hard to distinguish the trunk from the crown, were classified as shrubs.

^c From 1 = none, clean and flat break (e.g., mechanical trimming) to 6 = highly structured with furrows greater than 1 m.

^d 1 = more than 50% of the total length of the structure lacks shrub stratum (even holes filled with brambles or non-woody vegetation are still considered gaps); 2 = 25%–50%; 3 = 10%–25%; 4 = 5%–10%; 5 = < 5%; 6 = continuous and hole-free shrub layer.

Woody plant diversity indices

The sampling was restricted to ligneous plants because they are known to be one of the main limiting factors of HD settlement (BRIGHT *et al.*, 2006; EHLERS, 2012). To ensure reproducibility between the three types of structures, only the first metre of accessible vegetation within the width of the transect was systematically reported, with individual plant identification (CHANIN & GUBERT, 2012). However, because hedgerows are known to be particularly rare in trees, all identifiable ones were recorded indiscriminately for this type of structure (BENZ *et al.*, 2021; FOULKES *et al.*, 2013).

The taxonomic identifications were based on the determination key from the electronic version of *Flora Helvetica*, which is the main botanical

reference book in Switzerland (LAUBER *et al.*, 2018). The identified plants were recorded with the *FlorApp* mobile application tools developed by Info Flora. An individual statement was created for each transect, which allowed the extraction of the data directly in the “.csv” format at obs.infoflora.ch (INFO FLORA, 2022). Some taxa that include many cryptic species or hybrids were identified only to the genus level: riparian willows (*Salix* spp.), but distinguished from *Salix caprea*, and brambles (*Rubus* spp.), but separated from raspberries (*Rubus idaeus*). *Rubus* spp. young shrubs and trees smaller than 50 cm were not recorded (BERGAMINI *et al.*, 2020). Potential misidentifications were anticipated by removing from the datasets species present at a single transect (1/30) (MORTENSEN *et al.*, 2022; RAMAKERS *et al.*, 2014a).

The diversity of soft and hard fruits was considered a separate predictor for HD presence/absence (JUŠKAITIS, 2008; MORTENSEN *et al.*, 2022; RAMAKERS *et al.*, 2014a). Each recorded taxon was categorised as a hard or soft fruit species based on functional rather than botanical criteria – how HD feeds on the plant instead of how a human would categorise the fruit in its ripe state.

Over the last decade, Hill numbers have proved to be good indicators of diversity. They better reflect the relative distinctions between transects compared with their absolute difference. Above all, they have the advantage of resulting from a single equation that varies by a single coefficient. Therefore, all numbers have the same unit and easily calculable equivalences (ROSWELL

et al., 2021). Hill numbers (species richness, Shannon's diversity [D], and Simpson's D) (tab. 2) were computed for all woody species (EHLERS, 2012; ROSWELL *et al.*, 2021), hard fruit species, and soft fruit species separately (see appendix 2) (BRIGHT *et al.*, 2006; MORTENSEN *et al.*, 2022; RAMAKERS *et al.*, 2014a) Hill numbers were computed using the R package *iNEXT* (3.0.0) (CHAO *et al.*, 2022; HSIEH *et al.*, 2016a, 2016c).

Recorded plants were also sorted as tree or shrub species according to the growing mode that had most often been observed on the field (see appendix 2), and their Hill numbers were also calculated separately, for a total of 15 partially redundant plant diversity variables (tab. 2) (BERTOLINO *et al.*, 2017; BRIGHT *et al.*, 2006; JUŠKAITIS, 2008).

Table 2. List of plant diversity variables.

Diversity variable	Measurement method	Variable type	Scale
Diversity of all woody species (<i>Sp.R_W</i> – <i>Sha_W</i> – <i>Sim_W</i>)	Selective taxonomic identifications	Continuous quantitative	Richness: [Expected species number] Shannon and Simpson: [unscaled]
Diversity of all hard fruit species (<i>Sp.R_HF</i> – <i>Sha_HF</i> – <i>Sim_HF</i>)	Selective taxonomic identifications	Continuous quantitative	Richness: [expected species number] Shannon and Simpson: [unscaled]
Diversity soft fruit species (<i>Sp.R_SF</i> – <i>Sha_SF</i> – <i>Sim_SF</i>)	Selective taxonomic identifications	Continuous quantitative	Richness: [expected species number] Shannon and Simpson: [unscaled]
Diversity of tree species (<i>Sp.R_SF</i> – <i>Sha_SF</i> – <i>Sim_SF</i>)	Selective taxonomic identifications	Continuous quantitative	Richness: [expected species number] Shannon and Simpson: [unscaled]
Diversity of shrub species (<i>Sp.R_SF</i> – <i>Sha_SF</i> – <i>Sim_SF</i>)	Selective taxonomic identifications	Continuous quantitative	Richness: [expected species number] Shannon and Simpson: [unscaled]

Ecological network variable

Although estimations fluctuate across populations and between methods, it is commonly accepted that the mean territory size of the HD is generally about 1 ha (100×100 m). However, this territory can potentially extend in any direction (BRIGHT *et al.*, 2006; CHANIN & GUBERT, 2012; FEDYŃ *et al.*, 2021; HITCHCOCK, 2019; JUŠKAITIS, 2008; WHITE & HUNT, n.d.). For each structure, circular shapefiles with a 100 m radius centred on the transect centroid were used as a proxy for the “HD potential territory extent”. A detailed shapefile of the *ecological network* was obtained from the *Geomatics and Land Register Service of the Neuchâtel Canton*. The “ecological network cover” variable was computed as a cumulative area through an overlap analysis of the two above layers (QGIS DEVELOPMENT TEAM, 2022; SITN, 2022).

Light pollution variables

With the authorisation of the political authorities of Val-de-Ruz, the coordinates and lighting schedules of each streetlamp were obtained from the Groupe E SA company that supplies the energy and the facilities for the Val-de-Ruz street lightings (BONVIN *et al.*, 2020; GROUPE E SA, 2022). To quantify artificial light pollution, a “shortest line and profile from line analysis” approach was developed (see below). Lampposts were represented as circles with a 1 m radius (QGIS – “Buffer”) to account for any small inaccuracy of their coordinates or in the positioning of transects (QGIS DEVELOPMENT TEAM, 2022). Two shapefiles were created: “All Lampposts” and “Permanent

Lampposts”. To integrate the potential “background noise” from private light emissions, human infrastructure data were obtained from the GIS dataset swissTLM3D, which is freely available on the Swiss Confederation’s website (JURA TROIS-LAC PAYS DE NEUCHÂTEL, 2022). Therefore, the two shapefiles were “All Light Sources: Buildings + All Lampposts” and “Permanent Light Sources: Building + Permanent Lampposts” were.

Shortest line and profile from lines analyses

The five shortest direct lines from the transects ($100 \text{ m} \times 1 \text{ m}$ polygons) towards any object of the artificial light sources shapefiles (QGIS DEVELOPMENT TEAM, 2022) were calculated. Topography and vegetation can hinder the diffusion of light. To weigh this effect, the five shortest lines were projected on a three-dimensional raster including the ground elevation and the height of the canopy (NORTH ROAD, 2022). Thus, the projected length of the “transects – light source” distance increases with variations in elevation due to vegetation or topography. Transects with a greater average distance are assumed to be exposed to the fewest light emission sources (RANZONI *et al.*, 2019). The average of the five projected lines was computed for the “All Lampposts” and “Permanent Lampposts” shapefiles, resulting in the predictors Shrt_All_L & Shrt_Pe_L, respectively. The operations were repeated with the two shapefiles “All Light Sources: Buildings + All Lampposts” and “Permanent Light Sources: Building + Permanent Lampposts” to obtain the variables Shrt_All & Shrt_Pe, respectively (tab. 3).

Table 3. List of light pollution variables.

Light pollution variable	Variable type	Measurement method	Scale
Shortest distance to all light pollution sources: buildings + all lampposts (<i>Shrt_All</i>)^a	Continuous quantitative	Shortest line and profile from lines	Metre [m]
Shortest distance to permanent light pollution sources: buildings + permanent lampposts (<i>Shrt_Pe</i>)^b	Continuous quantitative	Shortest line and profile from lines	Metre [m]
Shortest distance to all lampposts (<i>Shrt_All_L</i>)^c	Continuous quantitative	Shortest line and profile from lines	Metre [m]
Shortest distance to permanent lampposts (<i>Shrt_Pe_L</i>)^d	Continuous quantitative	Shortest line and profile from lines	Metre [m]

Due to their redundancy, it was expected that only one of these variables would be significant for a single and same habitat model. The underlying assumptions were:

^a All potential sources of light pollution are likely to disturb the HD;

^b Constant emissions of the buildings are the very main source of annoyance;

^c All public lights are likely to disturb the HD;

^d Constant emissions of the permanent lampposts are the very main source of annoyance.

Analyses and habitat model

The final dataset contained 25 habitat variables (see Table 1 [$n = 5$], Table 2 [$n = 15$], Table 3 [$n = 4$] and *ecological network cover*), but most of them were obviously or potentially redundant, especially the diversity and the light pollution indices within their own category (CARTLEDGE *et al.*, 2021). To visually explore whether the distribution of the variables displayed trends in the differentiation between hedgerows, edges, and riparian vegetation, transect boxplots sorted by structure type were computed. Then, non-metric multidimensional scaling (NMDS) was used to determine whether, by modelling the transects according to the proportion of each plant taxon, it was possible to observe grouping by structure type. To assess which of the 25 predictive variables were significantly related to

the two main scales leading the distribution of the transects projected by their proportion of each plant taxon, and to compare their respective associations with these main dimensions, a second NMDS was conducted by adding these 25 factors to the model. Cleveland dot plots were used to identify potential outliers. Finally, pair plots were used to look for potential relationships between the predictors, such as positive or negative correlations (HARTMANN *et al.*, 2018; VAN MEERBEEK, 2022; ZUUR *et al.*, 2009).

Transect IDs were investigated as a potential random effect (BOLKER, 2015; CARTLEDGE *et al.*, 2021; RAMAKERS *et al.*, 2014a). Generalised linear mixed models (GLMMs) were used to deal with the binomial nature of the explanatory variable, namely HD presence/absence data. Based on the literature,

GLMMs are appropriate for computing the HD habitat model from footprint tunnel and nest research data alone or in combination (BULLION *et al.*, 2018; MORTENSEN *et al.*, 2022; RAMAKERS *et al.*, 2014a).

Before employing GLMMs, the relationships between the variables were explored, without including a random effect, using generalised linear models (GLMs) (*glm* in R) (R CORE TEAM, 2022). Potential collinearity was assessed by computing the variance inflation factor (VIF) (*imcdiag* in the *mctest* [v. 1.3.1] package) (IMDADULLAH *et al.*, 1983; ULLAH & ASLAM, 2018). Then, GLMMs were computed by integrating factors with potential random effects of the transects ID (*glmmTMB* in the *glmmTMB* [v. 1.1.5] package as well as the *MuMIn* [v. 1.47.1] package) (BROOKS *et al.*, 2017). GLMMs were compared using iterative reductionist and constructive approaches, that is, by progressively adding or removing predictors to the detection models and looking for the best one based on the lowest Akaike information criterion (AIC) value (BOLKER *et al.*, 2009). More methodical tools were used for multiple model comparisons (*dredge* and *get.models* in the *MuMIn* [v. 1.47.1] package) (BARTOŃ, 2022).

Post hoc tests were performed to assess the robustness of the best models (the *car*, *DHARMA* [0.4.6], *mgcv* packages) (FOX & WEISBERG, 2019; HARTIG, 2021; LEYING, 2021; R CORE TEAM, 2022; WOOD, 2011; ZUUR *et al.*, 2009). The effect curves of the significant variables were computed (*effects* in the *effects* package) (FOX, 2003; FOX & HONG, 2009; FOX & WEISBERG, 2018, 2019). A classification tree was produced to better appreciate the actual interactions between these variables as well as their respective impact in the habitat model (*tree* in the *tree* package) (RIPLEY, 2022). A preliminary test was used to evaluate the significance of the risk for spatial autocorrelation (*testSpatialAutocorrelation* in the *DHARMA* package) (HARTIG, 2021; HERTZOG, 2019; LEYING, 2021). Then, how detection data correlate

depending on their geographical proximity was modelled by using the coordinates of the transects with recorded presence as random variables into a GLMM (*fitme* in the *spaMM* package). The *Correlation by Distance*, i.e., HD detection relative to transect spatial proximity, was then computed (*MaternCorr* in the *MaternCorr* package) and plotted (*plot* in R) (HERTZOG, 2019; R CORE TEAM, 2022; ROUSSET & FERDY, 2014). Then, to assess whether the abundance or proportion of individual or multiple plant taxa could be considered a significant predictor potentially interacting with one or more of the other 25 predictor variables, all combinations were explored through GLMs and GLMMs with model selection tools (HARTIG, 2021; JUŠKAITIS, 2008; LEYING, 2021; MORTENSEN *et al.*, 2022; RAMAKERS *et al.*, 2014a).

RESULTS

Footprint tunnel survey

Overall, 251 papers with footprints were collected, of which 215 were attributed to “unidentified rodents” and 42 were identified as HD. Only three pieces of cardstock showed simultaneously footprints of both HD and “unidentified rodents”. None of the footprints could be attributed to either the edible or garden Dormice. The 42 HD footprints were collected over only six different transects (3 **E** & 3 **R**), and half of these provided HD footprints during the first survey week. The number of tunnels with HD detection data increased continuously throughout almost the entire sampling period, reaching 10 at the end of the survey (fig. 3). “Unidentified rodent” detections also increased over the survey period. On average, they were 4.6 times more numerous than the actual HD detections, with the largest difference in the fifth week (fig. 3). None of the footprints that were found in hedgerows could be attributed to the HD. Three transects – E 13, E 17, and R 24 (fig. 1) – each had a nest built in one of their footprint tunnels.

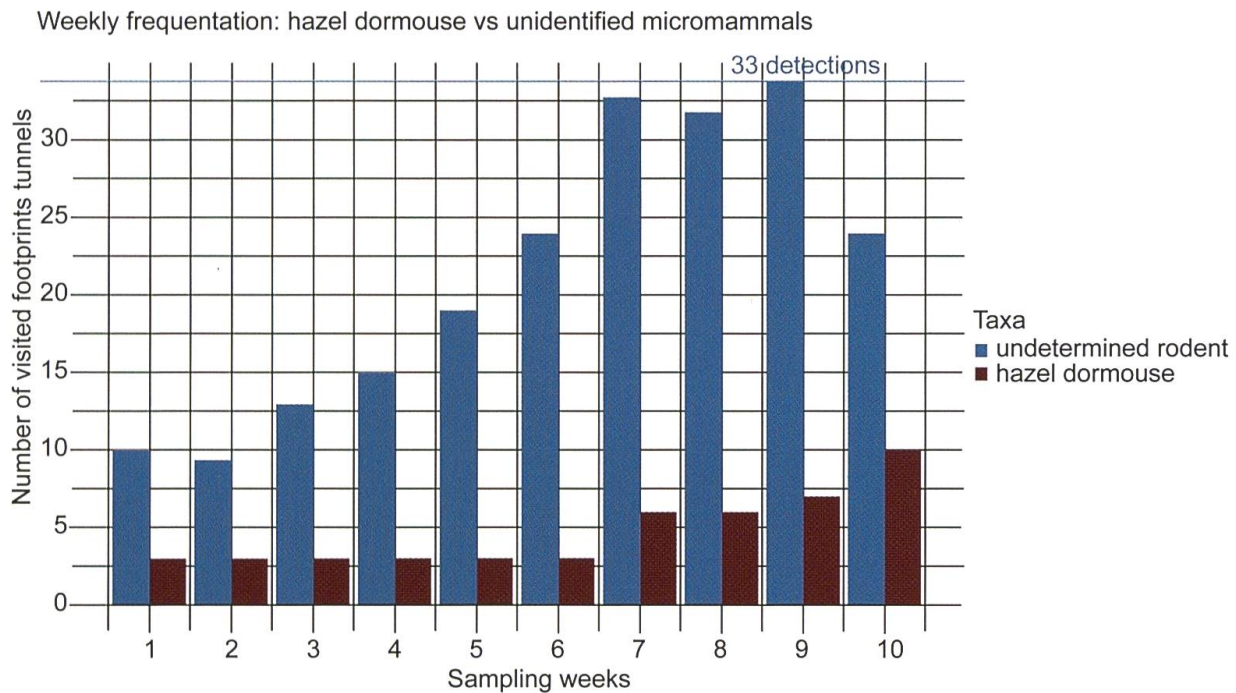


Figure 3. The number of weekly footprints sorted by taxonomic unit.

Nest research

A total of 16 nests were found over eight different transects, with five transects having two or more nest; their assumed usage, position in the vegetation, and composition type are presented in Table 4. The combined footprint tunnel and nest research data showed the presence of HD at 10 of the 30 woody structures sampled (4 E & 6 R) (fig. 4). While four transects had data from both methods, two transects provided only footprints, and four transects provided only nests. Except for the nests found in the footprint tunnels, over half of the nests (9/13, ~69%) were in

the HL. Just over half of all the nests (9/16, ~56%) were exclusively composed of grassy material. Notably, eight of these nests were found in the herbaceous strip, whereas the last grassy nest was found in the R24-T3 footprint tunnel. Of the remaining nests, three were made of mixed materials, three were distinctly layered, with a grassy inner ball covered with leaves, and one was composed exclusively of foliar material. Overall, only four nests were large enough (> 10 cm) to be considered potential breeding nests. While layered nests are assumed to be typically constructed for breeding purposes, only one of the four bigger nests presented this composition.

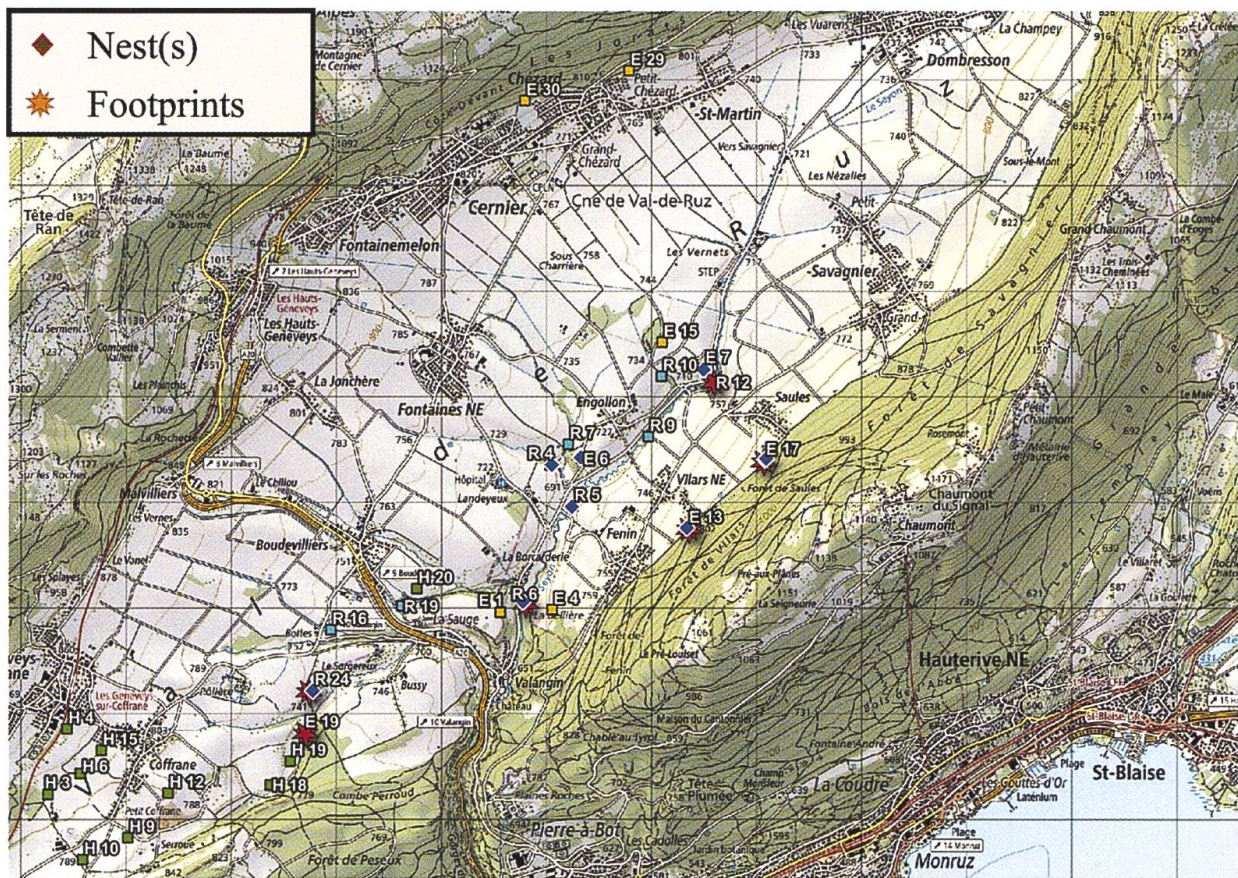


Figure 4. Distribution of the detection data by survey method.

Table 4. Nest characteristics.

Nest name	Nest use	Position in vegetation	Composition type
<i>E17-2</i>	Sleeping	SL	Mx
<i>E17-T2</i>	Sleeping	SL	Fl
<i>E6-1</i>	Sleeping	HL	Gr
<i>E6-2</i>	Sleeping	HL	Gr
<i>R4-1</i>	Sleeping	HL	Gr
<i>R4-2</i>	Breeding	HL	Gr
<i>R4-3</i>	Breeding	HL	Mx
<i>R4-4</i>	Sleeping	HL	Gr
<i>R5-1</i>	Sleeping	HL	Gr
<i>R5-2</i>	Sleeping	HL	Gr
<i>R5-3</i>	Sleeping	HL	Gr
<i>R6-1</i>	Sleeping	SL	Mx
<i>R7-1.1</i>	Sleeping	SL	Ly
<i>R7-1.2</i>	Sleeping	SL	Ly
<i>R13-T3</i>	Breeding	SL	Ly
<i>R24-T3</i>	Breeding	SL	Gr

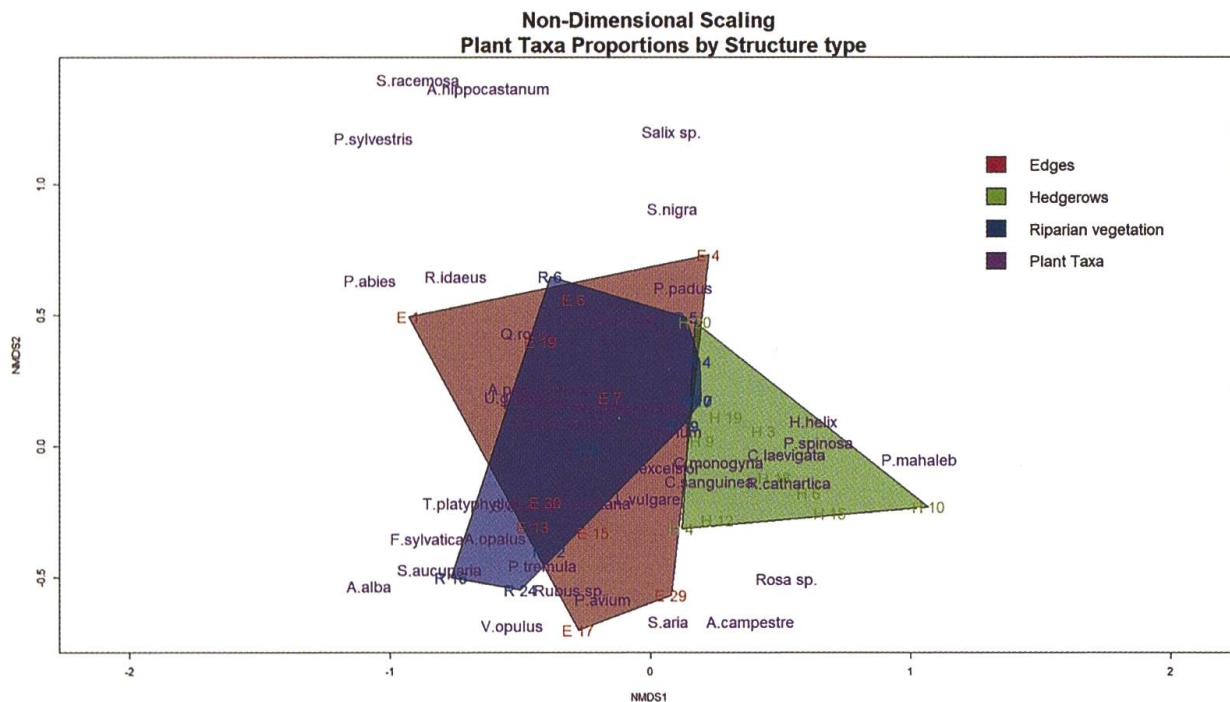


Figure 5. The first NMDS projection of the transects by plant taxon proportions and grouping by structure type.

DATA ANALYSES

Relationship between environmental variables

The boxplots highlighted a relatively clear separation of the mean HS for the edges and riparian vegetation transects, while the scores of hedgerows transects encompass those of the two other structure types. Hedgerows have a much lower mean HTT than the two other structure types, which display almost identical distributions (see appendix 3). We noted an identical trend in the diversity variables linked to the tree layer (Sp.R_T, Sha_T, Sim_T, Sp.R_HF, Sha_HF, and Sim_HF).

The first NMDS indicates that hedgerows are a type of structure apart from the edges and riparian transects. In contrast, the vegetation compositional range of riparian vegetation transects is largely encompassed by that of the edges (fig. 5).

We computed the second NDMS with all 25 predictors, but only those with a significant role in the distribution of transects by species proportion are shown by a vector that expresses their relationships with the two main dimensions. The HTT and the HS are strongly related to the grouping of the transects by structure type. The HS leads to the isolation of hedgerows as a particular structure type. Based on the Pearson correlation coefficients, we found a negative correlation between the HTT and the HS ($\text{cor} = -0.4392738$; $p = 0.01515^*$). The second NMDS also shows that the vectors of all the variables related to the tree layer, in terms of its diversity (Sp.R_T, Sha_T, Sim_T & Sp.R_HF, Sha_HF, and Sim_HF) and structure (HTT), have similar associations with the main dimensions of the model. In addition, Sha_HF returned identical but stronger information as Sp.R_T (fig. 6).

We found that indices for hard fruit, soft fruit, tree-growing, and shrub-growing taxa

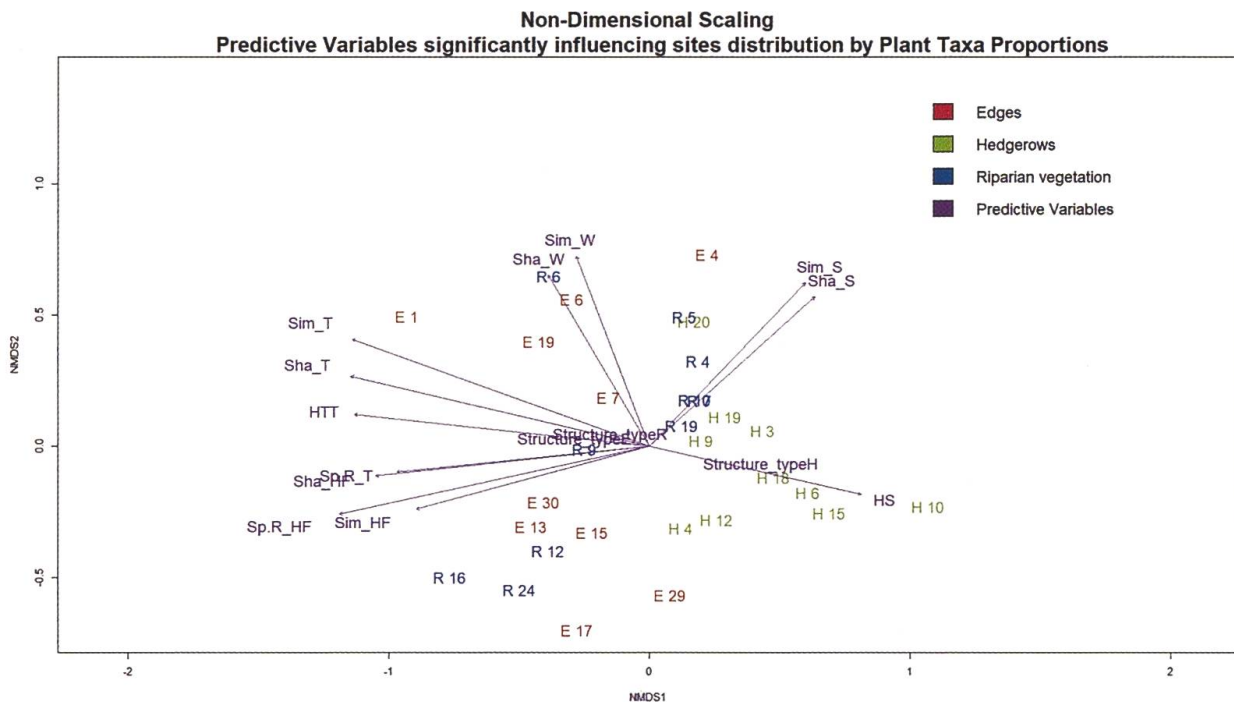


Figure 6. The second NMDS projection of the transects by plant taxon proportions and predictive variables (with colours based on the structure type).

correlate with the variables for all the woody species from which they are derived. On the other hand, we found a negative correlation between the diversity indices for hard fruit taxa and tree growing taxa and between soft fruit taxa and shrub-growing taxa. Nevertheless, the diversity indices of the hard and soft fruit taxa are quite distinct and do not correlate based on Pearson correlation coefficients or overlap on the NMDS; the same is true for the tree- and shrub-growing taxa.

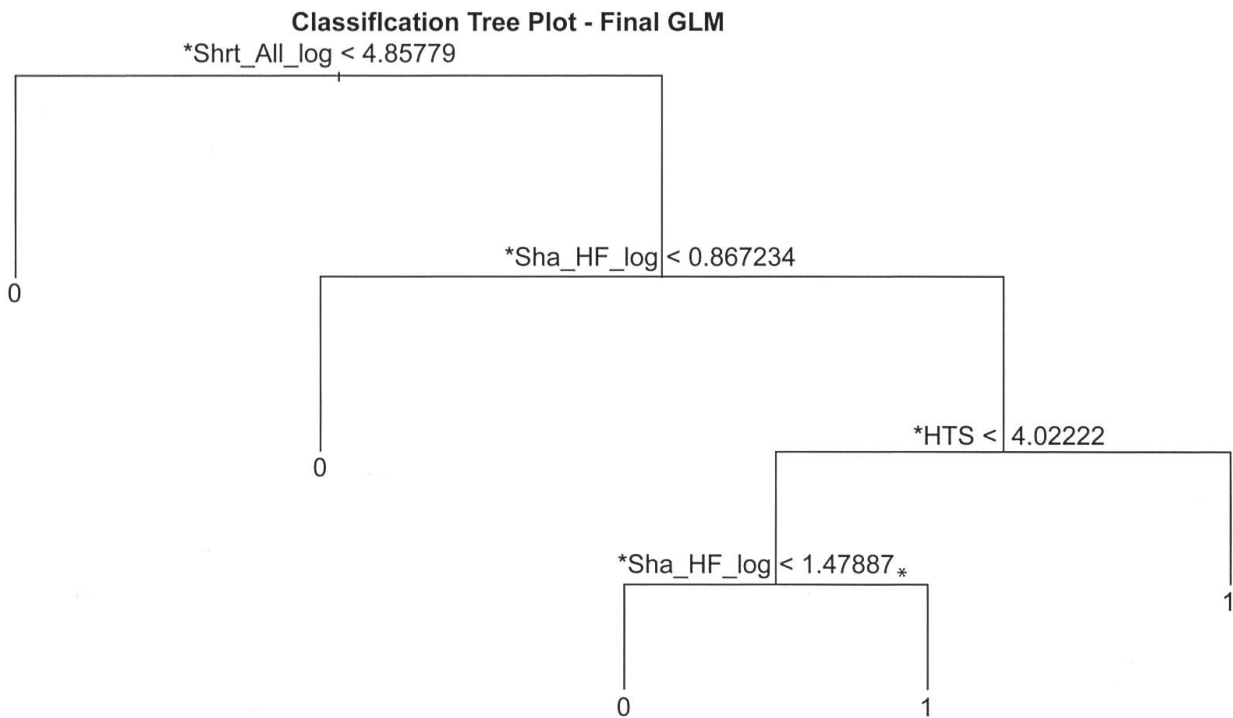
In summary, among the numerous structural and diversity variables generated, most are redundant (CARTLEDGE *et al.*, 2021). Regarding variables for light pollution, although undeniably redundant, the indices derived from the “shortest line and profile from line analysis” did not display severe outliers.

Regression models

GLMs and GLMMs suggested that the HTS, Shrt_All, and Sha_HF are the most significant predictors to detect the HD. However, we did not retain the transect IDs as a predictor because they induced statistically significant but meaningless intercepts, which had a negative impact on the robustness of the model. It seemed more appropriate and parsimonious to stick with GLMs (ZUUR *et al.*, 2009). VIF checks highlighted a collinearity issues in the GLM ($HD \sim HTS + Sha_HF + Shrt_All$), and *gam* tests highlighted the residuals of the Sha_HF and Shrt_All indices to satisfy the GLM assumption of linearity (ZUUR *et al.*, 2009). The final GLM (tab. 5) that indicates that the presence/absence of the HD is significantly and positively impacted by the mean HTS, the log-scaled Shannon’s D of hard fruit taxa, and the log-transformed mean shortest distance to all potential light-pollution sources ($HD \sim HTS + Sha_HF_log + Shrt_All_log$; AIC = 26.984; AICc = 28.6; Weights = 0.748).

Table 5. Final GLM.

	Estimate	Standard error	z value	Pr(> z)
(Intercept)	-33.586	13.200	-2.544	0.0109 *
Shrt_All_log	2.766	1.243	2.225	0.0261 *
HTS	2.410	1.288	1.872	0.0612 •
Sha_HF_log	6.622	2.901	2.283	0.0225 *

**Figure 7.** Classification tree plot of the final GLM.

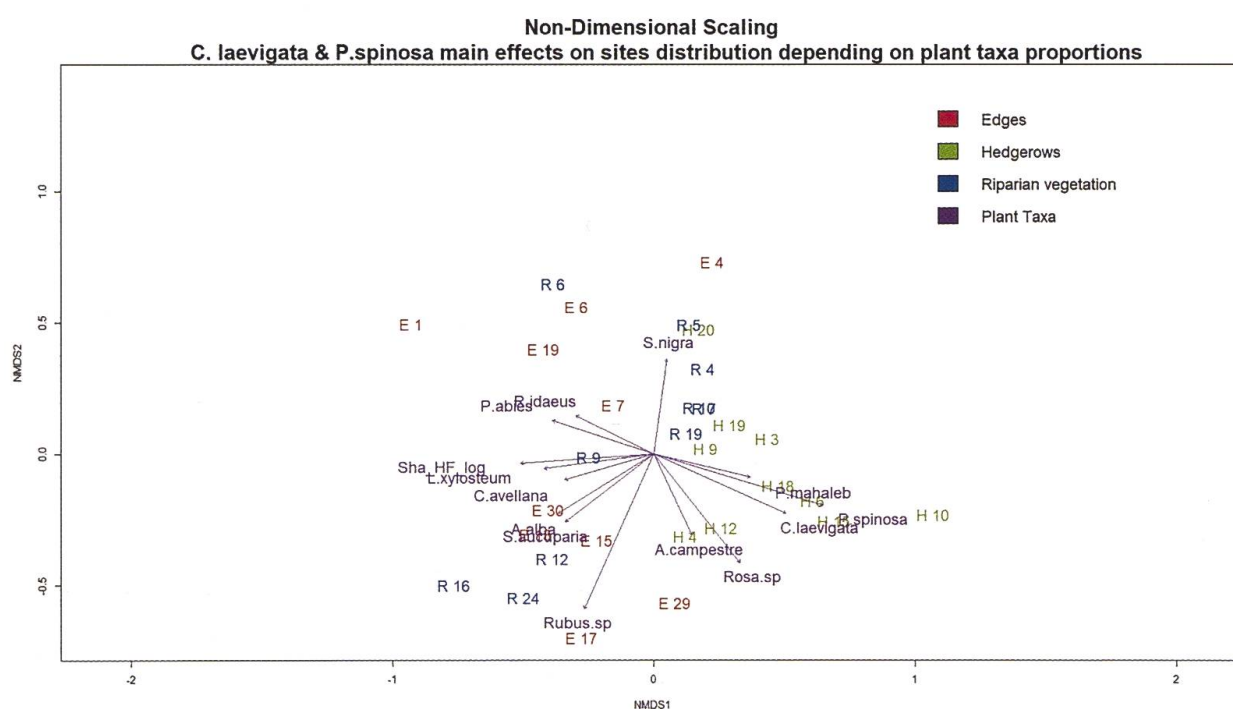
In the final GLM, the HTS is only marginally significant (with a p-value slightly higher than 0.05), but removing it resulted in less powerful models with lower AIC scores (ZUUR *et al.*, 2009). Likewise, deviance analyses, single term deletions, and the post hoc tests stressed the importance of the HTS for the robustness of the final GLM.

None of the GLMs showed a significant interaction between two predictors

regarding their potential influence on the presence or absence of HD (e.g., $HD \sim P1*P2$). The final GLM supports that each of the three predictors (HTS, Sha_HF_log, and Shrt_All_log) has a positive and significant effect on the probability of detecting the HD. The predictors HTS and Sha_HF_log are negatively correlated ($\text{cor} = -0.348$; $p = 0.05962\bullet$). The HTS is significantly correlated with the Shrt_All_log ($\text{cor} = 0.375$; $p = 0.04105*$).

Table 6. Significant *Prunus spinosa* and *Crataegus laevigata* GLMs.

	<i>P. spinosa</i> GLM (AIC = 28.933)			
	Standard error	z value	Pr(> z)	Pr(> z)
(Intercepts)	0.6420	0.6488	0.989	0.3224
<i>P. spinosa</i>	-287.0996	129.3710	-2.219	0.0265 *
	<i>C. laevigata</i> GLM (AIC = 34.411)			
	Standard error	z value	Pr(> z)	Pr(> z)
(Intercepts)	1.2132	0.7418	1.636	0.1019
<i>C. laevigata</i>	-3588.4135	1421.4517	-2.524	0.0116 *

**Figure 8.** The third NDMS projection of the transects by plant taxa whose proportions significantly ($p < 0.05$) affect the differentiation of transects (colours by structure type).

All of the terminal nodes of the classification tree are significant ($p < 0.05$), indicating that the threshold values returned by the model for the three variables are determinant for HD presence/absence (fig. 7). First, the *Shrt_All_log* score suggests that transects need to be at least $e(4.85779) \approx 130$ m away from any potentially

light-emitting facility for the HD to be present. If the HTS is higher than 4 m, then the HD might be detected when *Sha_All_log* is greater than $e(0.867234) \approx 2.4$. Such scores are small for the present dataset because the mean and median *Sha_All_log* are both about 3.7. When the HTS is under 4 m, the HD can

still be found if Sha_HF_log is greater than $e(1.47887) \approx 4.4$. The incidence that the three predictors independently have on the probability of HD presence/absence is not linear. Moreover, their respective effect curves display a steep sigmoidal appearance.

The risk of spatial autocorrelation was not significant ($p = 0.8434$). Two independent GLMs returned the proportion of *Prunus spinosa* and *Crataegus laevigata* as significant but negatively correlated with HD presence/absence (tab. 6). We did not find any significant interaction between either of these two species and the 25 predictor variables.

When we computed the proportion data of all woody taxa with an NMDS model, *P. spinosa* and *C. laevigata* returned a similar association with the main dimensions and seem strongly related to hedgerows (fig. 8). Projecting the median values of proportion for these two plant species depending on the type of linear structure, highlighted the proportion score of these two plants to be way higher in hedgerows transects than the values of the two structure types, which are comparable with each other (see appendix 3).

DISCUSSION AND CONCLUSIONS

Hedgerows as particular structures

Although we did not detect HD in hedgerows, they were the only type of structure to be distinguished by their compositional and structural vegetation properties. Our naturalistic criteria were too weak to encompass the variety of the woody patches in Val-de-Ruz, making our three categories unusable as predictors in the HD habitat model. The distinctive feature of the hedgerows seems to be their extremely sparse tree layer, no doubt due to management advice which suggests planting one tree approximately every 30 m (BENZ *et al.*, 2015, 2021; CAMPO, 2014; SORDELLO *et al.*, 2021). More multi-layered hedgerows should be promoted because they are most favourable for the

HD and biodiversity across its European distribution range (BENZ *et al.*, 2021; CAMPO, 2014; FOULKES *et al.*, 2013; JUŠKAITIS, 2008).

Hedgerows are also distinguished by their poorly diversified plant composition: they are dominated by *C. laevigata* and *P. spinosa*, which both have a negative, independent impact on the presence of the HD. The official Swiss guidelines for the creation and maintenance of hedgerows stress maintaining a high diversity of vegetation (BENZ *et al.*, 2021). However, the regional *ecological network* has its own conservation objectives and management criteria that must be considered (RÉPUBLIQUE DU CANTON DE NEUCHÂTEL, 2004; SITN, 2022):

1. Preserve the hygrophilous animal communities depending on the small water-courses (streams, drains) that run through the utilised agricultural area – especially the dusky large blue (*Phengaris nausithous*) and its host plant species the great burnet (*Sanguisorba officinalis*);
2. Restore the regional avifauna and, in particular, target the guild of birds linked to low and dense hedgerows that are rich in thorny shrubs.

It is likely that many thorny shrubs were planted to meet goal 2 (RÉPUBLIQUE DU CANTON DE NEUCHÂTEL, 2004). Although blackthorn and hawthorn serve as feeding sources and nesting sites for the HD, these two shrubs are neither its main nor preferred food sources. When the density of these shrubs is too high, they conflict with the HD's need for diversified habitats and lead to a reduced presence of rodents (BRIGHT *et al.*, 2006; JUŠKAITIS, 2008; RAMAKERS *et al.*, 2014a).

Even if the *ecological network* structures are not suitable for the HD to establish over a longer term, they still may help them to disperse through agricultural areas (CARTLEDGE *et al.*, 2021). The lack of connectivity is probably the reason why the HD was not detected in the three-lake region in the lower part of the canton of Neuchâtel (BLANT, 2015).

Most of the sampled hedgerows are grouped in the western part of Val-de-Ruz, but their inter-connectivity is far below the requirements of the HD (SITN, 2022). To be considered part of the *ecological network*, structures must be less than 200 m away from each other (RÉPUBLIQUE DU CANTON DE NEUCHÂTEL, 2004). In Val-de-Ruz, 200 m is rather the norm, and some hedgerows no longer than 100 m are very isolated from any other woodland patch (SITN, 2022). In forest habitats, the HD rarely crosses open areas of more than 3 m (Bright *et al.*, 2006), but in fragmented semi-natural environments, many observations suggest that dispersing males and juveniles could cross treeless landscapes over hundreds of metres (up to 500–700 m) (CHANIN & GUBERT, 2012; FEDYŃ *et al.*, 2021; JUŠKAITIS, 2008; TESTER, 2018) and sometimes even roads (BRIGHT *et al.*, 2006; CHANIN & GUBERT, 2012; DIETZ *et al.*, 2018a; FEDYŃ *et al.*, 2021; JUŠKAITIS, 2008). However, the diversity of the available studies, their methodologies, and the differences in habitats and habits between HD populations make it difficult to draw any conclusion on the HD's ability to disperse (JUŠKAITIS, 2008).

In spring 2021, students at the University of Neuchâtel used plywood tunnels and detected the HD in linear vegetation structures we would have qualified as hedgerows, with some even in direct continuity with the transects we studied. Some HD were able to settle, at least temporarily, in the hedgerows south of Val-de-Ruz (INFO FAUNA [CSCF & KARCH] & CCO-KOF, 2022b; JUŠKAITIS, 2008). Besides, all observations of HD reported over the past 20 years suggest that the species is restricted to the southern side of the valley (INFO FAUNA [CSCF & KARCH] & CCO-KOF, 2022b).

Given the status of the HD as an indicator species, many other taxa surely suffer from the above-mentioned overabundance of thorny shrubs as well as the lack of inter-connectivity between woody structures and, more globally, between the southern and northern sides of the valley (BRIGHT *et al.*,

2006; DIETZ *et al.*, 2018a; FEDYŃ *et al.*, 2021; HAAG, 2014; INFO FAUNA [CSCF & KARCH] & CCO-KOF, 2022b). The HD meets most of the criteria listed in the *Cantonal Ordinance on Ecological Quality of Neuchâtel* to be considered a target species for setting the goals of an *ecological network* (BRIGHT *et al.*, 2006; EHLERS, 2012; JUŠKAITIS, 2008; RÉPUBLIQUE DU CANTON DE NEUCHÂTEL, 2004). Reassessing the conservation objectives of the Val-de-Ruz *ecological network* by integrating the ecological requirements of the HD would benefit many other species. Thorny bush species are also important for the HD as a food source as well as a hiding and nesting place (BRIGHT *et al.*, 2006; EHLERS, 2012; FEDYŃ *et al.*, 2021; HAAG, 2014; JUŠKAITIS, 2008; TESTER, 2018). The guild of birds targeted by the actual objectives could benefit from an improvement in the structural and compositional properties of the woody structures, especially regarding food availability (BENZ *et al.*, 2021; BRIGHT *et al.*, 2006; JUŠKAITIS, 2008; RÉPUBLIQUE DU CANTON DE NEUCHÂTEL, 2004; TESTER, 2018; WHITE & HUNT, n.d.). Besides, the HD conservation measures are favourable for the dusky large blue (*P. nausithous*) (HAAG, 2014). While ensuring continuity between structures is not always possible, creating more small patches allows for “stepping-stone” movement that, although not optimal, would nevertheless increase the dispersal capacity of the HD (DIETZ *et al.*, 2018a; JUŠKAITIS, 2008).

In any case, the planted hedgerows may simply be too young to meet the HD requirements (e.g., temporary shelters, such as old hollow trees, required by dispersing HD juveniles) (BLANT *et al.*, 2012). It may take decades of extensive management for planted patches of vegetation to achieve the same compositional and structural properties as natural sites of the same age. Of note, the Val-de-Ruz *ecological network* only began to take shape in the 2010s (LUGON & BILAT, 2004; LUGON & JACOT-DESCOMBES, 2008).

Habitat models

Based on the results from the “correlation by distance” plot, we deemed the threshold of 100 m to be reliable for selecting a transect. We considered the potentiality that the proximity between two transects might have influenced the detectability of the HD to be negligible in the present study.

THE SIGNIFICANT VARIABLES OF THE FINAL GLM

Shortest distance to all light pollution

The classification tree model suggests that the structure must have a minimum score of $CT1 = 4.85779$ [$\log(m)$] for *Shrt_All_log*. If we back-transform this estimate, then the transect must be at least 130 m (~ 128.74 m) from any potential light pollution source. This distance is about 1.8–2.2 times lower than the mean (5.430653–228.3 m) or median (5.647083–283.46 m) of all transects. Therefore, although considered significant by the final GLM, the negative effects of light pollution appear to affect only a short range as many transects are far enough from any light sources to not reach the HD threshold for this criterion. Transects E 13 and E 17 are the most convincing examples of this view. These two occupied transects are both in continuity with the same edge overlooking the agglomerations of Vilars (NE) and Saules, respectively. Thus, they are both close to dwellings and exposed to all potential sources of anthropogenic disturbance, starting with light and noise pollution. In addition, these transects are located along a busy pathway and thus exposed to disturbances from walkers and their dogs, riders and horses, and cyclists. As predators of the HD, cats from nearby houses and farms are also likely to represent a threat (BEIER *et al.*, 2013; BRIGHT *et al.*, 2006; GOODWIN, HODGSON *et al.*, 2018; JUŠKAITIS, 2008; MÄLDIG, 2014; SORDELLO *et al.*, 2014; WEINBERGER & BRINER, 2022). These two transects illustrate that *Shrt_All_log* is not

an appropriate indicator at scales as small as those of the present study to isolate the light pollution effects. Indeed, at distances of hundreds of metres, the latter predictor necessarily encompasses all the above co-factors.

Given that almost all public or private buildings, as well as facilities, are potential light pollution sources, *Shrt_All_log* could also be interpreted as a proxy for urban density. A broad-scale study based on GIS data showed that UK HD populations are particularly impacted by the proportion of “urban areas” in the neighbourhood of their habitats (CARTLEDGE *et al.*, 2021). Although more general, these measures are usually considered to be an acceptable proxy for light pollution for want of anything better (SORDELLO *et al.*, 2021). In this respect, aerial pictures of Val-de-Ruz at night should be available around 2023–2024. Hence, other projects could try to reproduce the methods employed by RANZONI *et al.* (2019) and relate the HD distribution data to a more accurate light pollution index (BLANT, 2022; RANZONI *et al.*, 2019). Alternatively, if it is impossible to assess the emissions from each light source, it might be possible to systematically measure, using a lux meter, an index of actual emissions – that is, all the light that reaches a point. The average of several measurements taken along a transect would then constitute a convenient indicator of its exposure to light (OFEV, 2021).

The present results suggest that whether *Shrt_All_log* partly represents light pollution or more generally urban disturbance sources, these effects, though significant, are limited in scope. In addition, increasing the number of transects located within less than 100 m of dwellings ($n = 5$ and 3 are hedgerows) could reveal the presence of the HD in private gardens in Val-de-Ruz, a phenomenon that has been observed elsewhere in Europe (BLANT & ERNE, 2020; BRIGHT *et al.*, 2006; WEINBERGER & BRINER, 2022). This possibility could be explored in future HD projects,

but it would be crucial to choose survey sites with adequate levels of vegetation factors, especially for the height of the shrub layer and the diversity of trees.

Overall, these results do not allow for a satisfactory conclusion regarding the potential effects of light pollution on HD presence/absence. Further investigation comparing distinct species of micromammals will be necessary to discuss the potential status of HD as an indicator species regarding the impact of light pollution (SORDELLO *et al.*, 2014, 2021). For this endeavour, wider models encompassing distribution data and dark natural corridors derived from satellite images could be the most straightforward methodology (DIETZ *et al.*, 2018a; RANZONI *et al.*, 2019). Nevertheless, the results support the idea that if accounting for light pollution is important when designing an *ecological network*, much attention should be paid to the factors that make a habitat suitable, especially vegetation factors (SORDELLO *et al.*, 2014).

Diversity of hard fruit species and the height of the shrub layer

The Pearson correlation coefficients as well as the second NMDS projection strongly support the assumption that except for hazel trees, most of the hard fruit taxa in our dataset were part of the tree layer. Concerning vegetation indices, the structure must have a minimum score of Sha_HF_log CT2.1 = 0.867234 [no units] to have a chance of detecting the HD. This represents a quite low score compared with mean (1.17885) and median (1.303064). Then, the mean height of the top shrub layer must at least be about CT3 = 4.02222 [m], that is, slightly more than both the mean (3.682833) and median (3.66634). Besides, when the HTS is too small, a much higher Sha_HF_log CT2.2 of 1.47887 – 1.8 times higher than the previous threshold – may somehow counterbalance this deficiency. These results suggest that tree and shrub

layers can compensate for each other to meet the HD requirements.

These findings reopen the debate regarding the relationship between the lack of trees in hedgerows and the absence of HD detection. Indeed, the hedgerow mean (0.6746473) and median (0.6528548) Sha_HF_log are about 1.2 times lower than the first Sha_HF_log threshold CT2.1. Yet, it should be remembered that the HD depends on a greater diversity of plants in its habitat mostly because this ensures that, thanks to the different phenology of each plant species, food will be continuously available in its habitat throughout its period of activity (BRIGHT *et al.*, 2006; FEDYŃ *et al.*, 2021; GOODWIN *et al.*, 2020; JUŠKAITIS, 2008; MORTENSEN *et al.*, 2022; RAMAKERS *et al.*, 2014a). Once again, except for hazelnuts, the hard fruits on which the HD feeds, such as acorns, beechnuts, and samaras, are mainly produced by tree-growing species. Hard fruits are considered particularly important for the HD because they allow the species to build up more fat reserves than soft fruits (BRIGHT *et al.*, 2006). These energy reserves are crucial for its survival during winter. The above results could be interpreted as follows: if the diversity of hard fruit is sufficient, providing an uninterrupted sequence of highly nutritious food, at least during the autumn part of the HD's activity, then the species will be able to establish on the site despite a sub-optimal shrub layer (BRIGHT *et al.*, 2006; HAAG, 2014; WEINBERGER & BRINER, 2022).

The tree layer of the hedgerows could have the twofold disadvantage of being sparse and dominated by common or few identical species. In this respect, it could suffer from a comparable problem as the shrub layer, which is dominated by thorny bushes (ROSWELL *et al.*, 2021). Similarly, although no remarkable results emerged from the habitat model regarding the distribution of woody species, within the first NDMS projection, one can note that, except for cherries, trees are absent from the hedgerow

cluster (fig. 5). Still, hedgerows also displayed a lower mean (3.668552) and median (3.635234) HTS than the threshold node from the classification tree (appendix 3). Thus, if vegetation is the reason for the lack of detection of the HD in hedgerows, it is not only because of the poverty of the tree layer, but also because the shrub layer lacks the structural properties to compensate, in addition to the problems associated with the dominance of thorny bushes.

Although the separation of hard fruit versus soft fruit species is frequently evaluated in the literature as a potential explanatory factor for HD habitat models, these analyses generally only offer inconclusive results for the latter variables, either outweighed by the other factors or rejected outright. Thus, their actual effects have rarely been discussed (MORTENSEN *et al.*, 2022; RAMAKERS *et al.*, 2014a). Similarly, in the present study, it was not possible to consider Sha_HF_log as a predictor for hard fruit only rather than for the tree layer more generally.

Another failure of this study is the unexpected irrelevance of the unretained HH, mostly because of mowing issues. Indeed, we found most nests in the herbaceous strata from the vegetation structures. Therefore, future work should foresee such issues and give more attention to the relationship between HD presence/absence and the herbaceous layer's structural and compositional properties, which are largely understudied in the literature.

The *National Dormouse Monitoring Programme* that has followed UK HD populations since the 1990s targets almost exclusively broadleaved woodlands. Thus, as previously suggested, the most used monitoring methodologies, in terms of site selection and sampling device installation, are possibly biased by the UK literature, which is both the most developed and renowned. Hence, many habitat

models published so far, including the present work might have failed to encompass the full variety of site variables that influence the presence of the HD (CARTLEDGE *et al.*, 2021; JUŠKAITIS, 2008; RAMAKERS *et al.*, 2014a). As suggested by RAMAKERS *et al.* (2014), the presence of brambles in the herbaceous layer could compensate for the lack of hollow trees in more open structures such as hedgerows. Further investigation into this issue might help to improve the efficiency of future surveys. As suggested above, footprint tunnels could be more useful in the most forested sites, whereas simple nest searching would be sufficient for sites where the herbaceous stratum is more developed.

Although widely used in the past, nest research has lost popularity because it is considered more time-consuming and less effective than nest boxes/tubes, used for long-term monitoring, or footprint tunnels, used for shorter surveys (BRIGHT *et al.*, 2006; HAAG, 2014). Although these assertions have often been reported, data from *The Dormouse Conservation Handbook Second Edition* (BRIGHT *et al.*, 2006) and more recent work suggest that nest research is just as effective as footprint tunnels (BRIGHT *et al.*, 2006; BULLION *et al.*, 2018). Thus, based on the advice of local micromammal experts, searching nests seemed to be an effective way to complement the footprint tunnel survey data (BLANT, 2022). However, we could not identify individuals or extract counting data from footprints (BULLION *et al.*, 2018; CAPT, 2022; HAAG, 2014; MELCORE *et al.*, 2020a). Over one night, a single HD can build a sleeping nest, while a couple of HD might construct a breeding nest. Similarly, individuals usually alternate between several nests (2–3 to a maximum of 6) at the same time and use the same nest for only a few weeks (15–32 days, a maximum of 61 days) (JUŠKAITIS, 2008). Therefore, we considered nest discovery as simple presence/absence data.

Increase in frequenting footprint tunnels over time

Similarly to HAAG (2014), we observed a substantial increase in the detection probability over the last weeks of the survey in mid-September. HAAG (2014) provided three non-exclusive explanations for these observations.

1. **A habituation effect:** as the survey continues, the HD would progressively be less afraid of the unfamiliarity of the footprint tunnels in their environment and therefore more willing to explore them.
2. **A plant-related phenological effect:** considering the higher number of shrubs whose fruits ripen in the early autumn, the HD could be more active in the shrubby strata at this period and thus by the way more likely to pass through a tunnel.
3. **An HD-related phenological effect:** juveniles are known to disperse at the end of summer along natural structures, sometimes over more than a kilometre (up to 1200 m) and more individuals could pass through footprint tunnels on these occasion (HAAG, 2014).

This last suggestion is the only one reported elsewhere in the literature (BULLION *et al.*, 2018) and is also emphasised within the Swiss community of naturalists working on micromammals (BLANT, 2022; BULLION *et al.*, 2018). BULLION *et al.* (2018) combined nest boxes and tubes with footprint tunnels and performed the survey from April to November. There was a similar detection peak during autumn, but also another one in late spring. BULLION *et al.* (2018) and HAAG (2014) support the dispersion of younglings as the best explanation for the autumnal detection peak. Longer-term monitoring based on nest boxes also records two annual peaks in spring and autumn. According to the demographic data, the spring peak corresponds with the HD (re)ensuring their territory after

hibernation, while the autumn peak is attributable to dispersing juveniles (JUŠKAITIS, 2008). Therefore, footprint tunnel detection peaks are clearly linked to the seasonal phenology and life history traits of the HD (BRIGHT *et al.*, 2006; BULLION *et al.*, 2018; HAAG, 2014; JUŠKAITIS, 2008).

No survey effort should be wasted during periods when, based on nest box/tube studies, there are lower detection rates:

1. **In early spring**, when HD are still occupying their hibernation nests while waiting to find the right site to build their summer nest;
2. **At the height of summer**, when the species is normally well established and thus less mobile or potentially reduces its activity due to high temperatures;
3. **In late autumn**, when the species is already occupying its hibernation nest (BRIGHT *et al.*, 2006; HAAG, 2014; JUŠKAITIS, 2008).

The survey schedule could be adapted to the two detection peaks by splitting up the sampling period between spring and autumn. For footprint tunnels, BULLION *et al.* (2018) recommended two 1.5-month periods around May and between September and October (BULLION *et al.*, 2018).

Some researchers have argued that detections obtained during the dispersal period cannot be considered as presence data. As explained above, unlike methods implying direct observation of nests, footprints do not provide reliable occupancy data (BAILEY & ADAMS, 2005; BULLION *et al.*, 2018). Still, it should be noted that the absence of nests can also be explained by the fact that the HD sometimes nests in tree cavities (BRIGHT *et al.*, 2006; BULLION *et al.*, 2018; JUŠKAITIS, 2008; RAMAKERS *et al.*, 2014a). If one wants to rely on footprint tunnels only, the autumn survey should be conducted before the spring

survey. Thus, if individuals overwintered and footprints are found in both autumn and spring, such replicated detections could be considered occupancy data (BRIGHT *et al.*, 2006; BULLION *et al.*, 2018; JUŠKAITIS, 2008).

Rather than adapting the survey schedule to activity peaks, BULLION *et al.* (2018) suggested a more flexible approach with adaptable sampling periods. Because footprint methods only provide annual presence/absence data, the survey period could be limited to a maximum of three consecutive months between May and October, and stop pointlessly collecting tracks where individuals have already been detected (BAILEY & ADAMS, 2005; BULLION *et al.*, 2018). A larger number of potential sampling sites could be planned, and the location of the footprint tunnels could be changed as new detections are made. The sampling effort would remain constant but could cover a larger study area. Still, we suggest that such a flexible survey should involve two 1.5-month periods over the seasonal detection peaks rather than over three consecutive months.

Weather effects

The absence of HD detection in hedgerows in the present work could be related to seasonal stochastic factors (AL-FULAIJ *et al.*, 2018; BRIGHT *et al.*, 2006; CARTLEDGE *et al.*, 2021; JUŠKAITIS, 2008). In Switzerland, summer 2022 was the second warmest since measurements were first taken in 1864. Three consecutive heatwaves occurred in just over two months, in mid-June, mid-July, and early August. The extreme temperatures and resulting drought have had many economic, social, and especially environmental consequences (MÉTÉOSUISSE, 2022). Thus, the vegetation was already damaged when the footprint tunnel survey started in mid-July. Therefore, it is likely that, even before the present study started, any HD established in the hedgerows could have suffered a break in the continuity of resource availability,

which is normally essential to their survival (BRIGHT *et al.*, 2006; FEDYŃ *et al.*, 2021; MORTENSEN *et al.*, 2022).

HD metabolism is particularly sensitive to weather and temperature changes and is highly impacted when conditions deviate from seasonal norms. Hence, while warmer summer conditions are usually associated with better living and breeding conditions for the HD, stronger heatwaves might also be unfavourable for the species, forcing it to increase its daily torpor time to save energy, but delaying its phenology (BRIGHT *et al.*, 2006; GOODWIN, SUGGITT *et al.*, 2018).

Direct observations of living individuals

We made a total of four direct observations of HD in broad daylight. We could observe the “immobility” behaviour of two individuals – quickly freezing in the vegetation as soon as it was seen and remaining motionless for minutes unless the observers decided to withdraw. According to Swiss field biologists, such “immobility” behaviour is common in glirids as a strategy to avoid predators (BLANT, 2022). However, we found nothing on this subject in the international literature. An investigation would be necessary to attest to this behaviour and to determine its real function.

Conservation implications

The present work provides a better idea of the HD distribution in Val-de-Ruz. Moreover, if we only rely on the size of the nests, up to four of them may be considered proof of a reproduction event. However, we found two at the same site that were surely built by the same individual(s) (JUŠKAITIS, 2008). Nevertheless, the three transects with potential breeding data suggest that reproduction occurs over a relatively large extent of the species distribution within the sampling area. Therefore, these three probable breeding

strongholds should be given particular attention in future projects involving this species.

The present work provides useful information for the future conservation of HD in the Val-de-Ruz and to safeguard Swiss populations. As mentioned above, the detection data from the last 20 years suggest that the HD populations in Val-de-Ruz are limited to natural structures in connection with the forest overlying the anticline in the south of the valley (INFO FAUNA [CSCF & KARCH] & CCO-KOF, 2022b). Thus, any longer-term HD conservation project should start by reinforcing the populations in this area, before progressively attempting to increase the distribution of the species, by enriching and increasing the vegetation structures up to their junction with the northern side of the valley. Besides, the Val-de-Ruz *ecological network* is already in itself a long-term conservation project. As mentioned previously, its goals could be smoothly redesigned to better suit the needs of the HD. This redesign would benefit many other species without compromising its initial objectives for some taxa.

In the longer term, Val-de-Ruz could become a reservoir for HD populations at least on the scale of the canton of Neuchâtel. In the context of the linear structures that form the Val-de-Ruz *ecological network*, the results of the present study suggest that priority should be given to increasing both the average height of the shrub layer and the diversity of hard fruit, or tree species in general. However, these two shrub and tree strata compete with each other and innovative management practices, validated by HD feedback monitoring, may be required to find the right balance (RAMAKERS *et al.*, 2014a). Therefore, if more comprehensive management guidelines were to be formulated for the conservation of HD in the canton of Neuchâtel or even for Switzerland, they should be developed in such a way as to help stakeholders adapt their practices to each structure on a case-by-case basis. Our results show that the

HD does not necessarily need the shrub and tree layer to be in equilibrium; it can settle at sites where only one of the two strata has rich structural and compositional vegetation properties. The classification tree (fig. 7) supports the idea that the height of the shrub layer, and probably its structure in general, should be the main priority.

The Swiss association Pro Bliche has already published guidelines for conservation of the HD. This document is part of a larger HD conservation project of unprecedented scope in Switzerland, but no survey results have been published yet (as of spring 2023). Similarly, these management guidelines only address silvicultural practices and are therefore limited to forests. Semi-natural structures from agricultural landscapes and other less-studied habitats discussed in the present work would require further research to define management guidelines that meet the needs of the Swiss HD populations (HAAG, 2014; TESTER, 2018). In any case, and even more so considering climate change, it is essential to engage policies to further preserve linear vegetation structures and to (re)create new ones (VANNESTE *et al.*, 2020).

Besides creating or improving natural structures, more direct conservation measures could be put in place (BRIGHT *et al.*, 2006). In this regard, decades of experience accumulated by the UK *National Dormouse Monitoring Programme* stresses that installing and maintaining wooden nest boxes where the species is present allows the population density to increase beyond the initial carrying capacity of the habitats. The availability of suitable nesting sites could constitute a limiting factor for the dispersal of the species. Juveniles depend upon these shelters as relays to move from their birthplace to a new territory (BRIGHT *et al.*, 2006; BULLION *et al.*, 2018; JUŠKAITIS, 2008).

As stated above, hollow trees were potentially insufficiently represented in hedgerows.

Similarly, the discovery of HD nests in the footprint tunnels may reflect the lack of suitable natural shelter in some vegetation structures of the Val-de-Ruz, although the latter potentially display adequate levels for other ecological factors.

Thus, by providing more nesting opportunities, nest boxes would allow a local increase in the breeding rate, which would facilitate the maintenance of individuals in existing, even sub-optimal, natural structures, pending their improvement and expansion (BRIGHT *et al.*, 2006; BULLION *et al.*, 2018; CARTLEDGE *et al.*, 2021; JUŠKAITIS, 2008; RAMAKERS *et al.*, 2014a).

Swiss HD populations are poorly known, and nesting devices are the best way to simultaneously obtain occupancy, behavioural, physiological, and demographic data with a limited disturbance to the species. Such information will be essential to develop consistent conservation policies (BRIGHT *et al.*, 2006; CAPT, 2022; HAAG, 2014). However, nesting devices are more expensive than footprint tunnels, require at least equivalent if not more sampling effort, and meet resistance from landowners who are more reluctant to accept permanent setups on their land (MELCORE *et al.*, 2020a). Thus, a longer-term and larger-scale HD conservation project will require specific financial, political, and societal support from the public authorities – the confederation, the cantons, the communes, the non-governmental organisation, or even the academic world (HAAG, 2014). However, even a conservation project combining measures for habitat protection and expansion with population enhancement approaches is not certain to succeed in preserving the HD. Indeed, despite considerable efforts the UK has invested, over the last 30 years, to monitor and safeguard the HD, its population continues to decline (CARTLEDGE *et al.*, 2021). Thus, once again, given the poor knowledge available in Switzerland about the species,

time, money, and effort should be invested quickly and extensively. Indeed, the latter may be much more threatened than estimated so far, and some local populations may disappear without anyone noticing (CAPT, 2022). Unknown populations cannot be protected from habitat loss, fragmentation, and human development in general. Therefore, every area with the potential presence of the HD should ideally benefit from such survey measures and patches with proven occupancy would deserve further investigations to improve knowledge about Swiss populations (BULLION *et al.*, 2018).

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ADDITIONAL INFORMATION

We invite interested stakeholders to request the full version of this master's thesis from the main author at vaudrozc@gmail.com. It contains more details about the present results and refers to additional Appendices that are not mentioned here. Likewise, we created a document with Supplementary Materials that explores additional themes, notably the problems and advantages related to the aseptic footprint tunnel method that we pushed to scales far beyond those reported in the literature. The Supplementary Materials also provide more information about the methods and the results for nest searching. Finally, most of the R code used to compute the models and graphs presented is available upon request.

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APPENDICES

Appendix 1. Coordinates of the centroids from the sampled transects (SCR: CH1903+/LV95 – Certified ID: EPSG: 2056)

Structure ID	X coordinate	Y coordinate
E 1	2559544.819517683237791	1207952.641801834106445
E 4	2560056.591622132342309	1207991.470779165392742
E 6	2560333.750949238892645	1209433.241500731324777
E 7	2561503.262822267599404	1210258.148345386376604
E 13	2561334.203301175031811	1208762.020191887393594
E 15	2561108.629180243238807	1210507.775680356193334
E 17	2562058.770838739816099	1209389.638052079360932
E 19	2557678.134998660534620	1206824.087216615676880
E 29	2560785.755421974230558	1213076.873743712436408
E 30	2559795.296295429114252	1212795.813631420023739
R 4	2560035.883922945242375	1209342.606399030657485
R 5	2560257.431219057645649	1208958.605796741554514
R 6	2559798.558046039193869	1208023.306558905867860
R 7	2560203.340296792797744	1209551.843660128535703
R 9	2560981.214267117436975	1209615.372574301203713
R 10	2561085.748910063412040	1210188.493165389401838
R 12	2561594.884064341895282	1210126.339626439381391
R 16	2557947.739432344678789	1207801.104895643657073
R 19	2558618.759836826939136	1208008.683150129392743
R 24	2557784.754054839257151	1207206.100120541173965
H 3	2555252.937006151303649	1206238.916925766505301
H 4	2555426.785965804941952	1206862.868568225298077
H 6	2555564.289899567142129	1206426.265968166291714
H 9	2556009.497873190324754	1205839.025003226008266
H 10	2555577.526741995941848	1205616.754942553350702
H 12	2556407.492587423883379	1206240.834835649700835
H 15	2555758.054649814497679	1206661.309220794821158
H 19	2557564.245474546216428	1206556.586082802619785
H 20	2558762.177287098951638	1208173.435879231663421
H 18	2557356.761866690590978	1206327.072623200714588

Appendix 2. Classification of the recorded plant species into ecological categories

We classified soft fruits as all species for which the HD do not need to gnaw lignified plant tissues to access calorific parts. Therefore, we classified legumes (*Populus* spp., *Salix* spp., and *Euonymus* sp.) as soft fruit taxa, given that *Salix* sp. fruits are eaten unripe by the HD. On the other hand, we classified species as hard fruits if the HD had to gnaw lignified parts to access the edible parts. For example, we classified cones of conifers as hard fruit (BRIGHT *et al.*, 2006; MORTENSEN *et al.*, 2022). While some taxa such as *Salix* spp. can be classified as soft fruits because the HD feed on the unripe pods – even though the ripe fruit becomes ligneous – the reverse situation is not possible. The categorisations below are based on an extensive literature review. We searched Google Scholar by using the following reproducible formulation to search for each genus and species: “genus name/species binomial name” or “English vernacular name”+ “hazel dormouse” (e.g., “*Corylus avellana*” or “hazel tree” + “hazel dormouse”). Contrary to what RAMAKERS *et al.* (2014) proposed, this extensive literature search showed that it was somewhat futile to create an explanatory variable

by grouping plant species considered to be potential food sources for the HD. Indeed, the studies from the HD’s distribution range include evidence that the HD eats almost all the ligneous species recorded in the present study. Thus, while the HD is classified as a specialist regarding its habitat needs, it is omnivorous and rather classified as a generalist or opportunistic species regarding its foraging behaviour (BRIGHT *et al.*, 2006; CHANIN & GUBERT, 2012; DIETZ *et al.*, 2018a; GOODWIN *et al.*, 2020; RAMAKERS *et al.*, 2014a). Unlike Mortensen *et al.* (2022), who classified the plants they recorded into four groups (hard masts, soft masts, conifers, and capsules and legumes), we restricted the categorisation of woody plants to soft and hard fruits. Considering the small dataset ($n = 30$), multiplying the number of categories would only increase the dispersion and prevent any significant outcome. In the same way, by basing the classification on the HD foraging habits, it seemed superfluous to increase the number of guilds included in the model.

The main inspiration for the classification of the sampled species into two categories – hard fruit and soft fruit taxa – is *The Common Dormouse Muscardinus avellanarius: Ecology, Population Structure and Dynamics* (JUŠKAITIS, 2008, p. 60).

Appendix 3. Boxplots of variables with trends in their mean distribution
by structure type

Plant taxon	Ecological relationship with the hazel dormouse	Source(s)	Food category	Growth type
<i>Abies alba</i>	Plausible shelter (limited density) and source of arthropod prey There is a lack of data on the role of conifers in foraging of the HD Used as a nesting support	(BRIGHT <i>et al.</i> , 2006; GOODWIN, HODGSON <i>et al.</i> , 2018; JUŠKAITIS, 2008)	Hard fruit	Tree
<i>Acer</i> spp. ^a <i>Acer campestre</i> <i>Acer opalus</i> <i>Acer platanoides</i> <i>Acer pseudoplatanus</i>	Actual food source	(BRIGHT <i>et al.</i> , 2006)	Hard fruit	Tree
<i>Aesculus hippocastanum</i>	Sweet chestnut flowers and hard fruit (<i>Castanea sativa</i>) are eaten by HD, but no evidence for the horse chestnut fruit	(BRIGHT <i>et al.</i> , 2006) No evidence in the literature regarding a role in foraging or particular prominence in the habitat	Hard fruit	Tree
<i>Alnus glutinosa</i>	Actual food source Correlated with habitat occupancy	(JUŠKAITIS, 2008)	Hard fruit	Tree
<i>Cornus sanguinea</i>	Potential food source	(GOODWIN <i>et al.</i> , 2020)	Soft fruit	Shrub
<i>Corylus avellana</i>	Actual food source Used as nesting support and its leaves are used as nesting material	(BRIGHT <i>et al.</i> , 2006; JUŠKAITIS, 2008)	Hard fruit	Shrub
<i>Crataegus</i> spp. ^b <i>Crataegus laevigata</i> <i>Crataegus monogyna</i>	Actual food source Used as a nesting support	(BRIGHT <i>et al.</i> , 2006; GOODWIN <i>et al.</i> , 2020; JUŠKAITIS, 2008)	Soft fruit	Shrub
<i>Euonymus europaeus</i>	Actual food source	(JUŠKAITIS, 2008)	Soft fruit	Shrub
<i>Fagus sylvatica</i>	Potential food source Used as nesting support and its leaves are used as a building material	(BRACEWELL & DOWNS, 2017; JUŠKAITIS, 2008; MORTENSEN <i>et al.</i> , 2022)	Hard fruit	Tree
<i>Fraxinus excelsior</i>	Actual food source Used as a nesting material source and a nesting support	(BRIGHT <i>et al.</i> , 2006; GOODWIN <i>et al.</i> , 2020; JUŠKAITIS, 2008)	Hard fruit	Tree
<i>Hedera helix</i>	Little is known Used as a nesting support No evidence in the literature regarding a role in foraging	(BRIGHT <i>et al.</i> , 2006; JUŠKAITIS, 2008)	-	Shrub
<i>Ligustrum vulgare</i>	No evidence in the literature regarding a role in foraging	-	-	Shrub

Plant taxon	Ecological relationship with the hazel dormouse	Source(s)	Food category	Growth type
<i>Lonicera xylosteum</i>	Actual food source Used as a nesting material source, a nesting support, and to provide habitat	(BRACEWELL & DOWNS, 2017; BRIGHT <i>et al.</i> , 2006; DALLMEIER & MORGAN, 2015; GOODWIN <i>et al.</i> , 2020; GOODWIN, SUGGITT <i>et al.</i> , 2018; JUŠKAITIS, 2008)	Soft fruit	Shrub
<i>Picea abies</i>	Actual food source Important habitat provider and nesting site	(BRIGHT <i>et al.</i> , 2006; CHANIN & GUBERT, 2012; JUŠKAITIS, 2008)	Hard fruit	Tree
<i>Pinus sylvestris</i>	Actual food source This could therefore also be the case for <i>P. sylvestris</i> . Used as a nesting support	(BRIGHT <i>et al.</i> , 2006; CHANIN & GUBERT, 2012)	Hard fruit	Tree
<i>Populus tremula</i>	Actual food source Used as a nesting material and a nesting support	(Axel KRANNICH <i>et al.</i> , 2014; BRIGHT <i>et al.</i> , 2006; EHLERS, 2012; JUŠKAITIS, 2008)	Soft fruit	Tree
<i>Prunus spinosa</i>	Actual food source Used as a nesting support	(BRIGHT <i>et al.</i> , 2006)	Soft fruit	Shrubs
Wild cherries ^c <i>Prunus avium</i> <i>Prunus mahaleb</i> <i>Prunus padus</i>	Actual food source	(FEDYŃ <i>et al.</i> , 2021; JUŠKAITIS, 2008)	Soft fruit	Tree
<i>Quercus robur</i>	Actual food source (inflorescences and fruits) Used as a nesting material source, a nesting support, and to provide habitat	(GOODWIN <i>et al.</i> , 2020; JUŠKAITIS, 2008; MORTELLITI <i>et al.</i> , 2012)	Hard fruit	Tree
<i>Rhamnus cathartica</i>	Actual food source Used as a nesting support	(JUŠKAITIS, 2008)	Soft fruit	Shrub
<i>Ribes alpinum</i>	Actual food source (<i>R. nigrum</i>)	No evidence in the literature regarding a role in foraging or particular prominence in the habitat	Soft fruit	Shrub
<i>Rubus idaeus</i>	Actual food source (inflorescence and fruits) Presence correlated with nesting site selection	(JUŠKAITIS, 2008)	Soft fruit	Shrub

Plant taxon	Ecological relationship with the hazel dormouse	Source(s)	Food category	Growth type
<i>Rubus</i> spp.	Actual food source Presence correlated with nesting site selection	(BRACEWELL & DOWNS, 2017; BRIGHT <i>et al.</i> , 2006; CHANIN & GUBERT, 2012; DALLMEIER & MORGAN, 2015; EHLERS, 2012; FEDYŃ <i>et al.</i> , 2021; GOODWIN <i>et al.</i> , 2020; GOODWIN, HODGSON <i>et al.</i> , 2018; JUŠKAITIS, 2008; MORTENSEN <i>et al.</i> , 2022; RAMAKERS <i>et al.</i> , 2014a)	Soft fruit	Shrub
<i>Rosa</i> sp. ^d	Actual food source Used as a nesting support	(BRIGHT <i>et al.</i> , 2006)	Soft fruit	Shrub
<i>Salix caprea</i>	Actual food source (inflorescences and fruits)	(BRIGHT <i>et al.</i> , 2006; JUŠKAITIS, 2008)	Soft fruit	Tree
<i>Salix</i> spp.	Actual food source (inflorescences and fruits)	(BRIGHT <i>et al.</i> , 2006; GOODWIN <i>et al.</i> , 2020; JUŠKAITIS, 2008; MORTENSEN <i>et al.</i> , 2022)	Soft fruit	Shrub
<i>Sambucus</i> spp. ^e <i>Sambucus nigra</i> <i>Sambucus racemose</i>	Actual food source	(JUŠKAITIS, 2008; MORTENSEN <i>et al.</i> , 2022)	Soft fruit	Shrub
<i>Sorbus</i> spp. ^f <i>Sorbus aria</i> <i>Sorbus aucuparia</i>	Actual food source Used as a nesting material source	(GOODWIN <i>et al.</i> , 2020; JUŠKAITIS, 2008; MORTENSEN <i>et al.</i> , 2022)	Soft fruit	Shrub
<i>Tilia platyphyllos</i>	Actual food source Used as a nesting material and nesting support and to provide habitat	(JUŠKAITIS, 2008)	Hard fruit	Tree
<i>Ulmus glabra</i>	No evidence in the literature regarding a role in foraging	-	-	Tree
<i>Viburnum</i> sp. <i>Viburnum lantana</i> <i>Viburnum opulus</i>	Actual food source Used as a nesting material source	No evidence in the literature regarding a role in foraging or particular prominence in the habitat	Soft fruit	Shrub

^a All sycamores (*Acer* spp.) are ecologically equivalent concerning HD requirements. Indeed, although they differ in leaf and fruit shape, size, and soil preference, researchers have considered them at the genus level to assess their relationship with the HD (BRIGHT *et al.*, 2006; GOODWIN, SUGGITT *et al.*, 2018).

Furthermore, the flowering and fruiting seasons of the four species largely overlap, making them even more ecologically similar to the HD (LAUBER *et al.*, 2018).

^b Hawthorns (*Crataegus* spp.) are also similar ecologically, producing soft red fruits and, thanks to their spines, may provide potentially suitable shelters for the HD (BRIGHT *et al.*, 2006; EHLERS, 2012). Moreover, the phenology of these diverse species overlaps (LAUBER *et al.*, 2018).

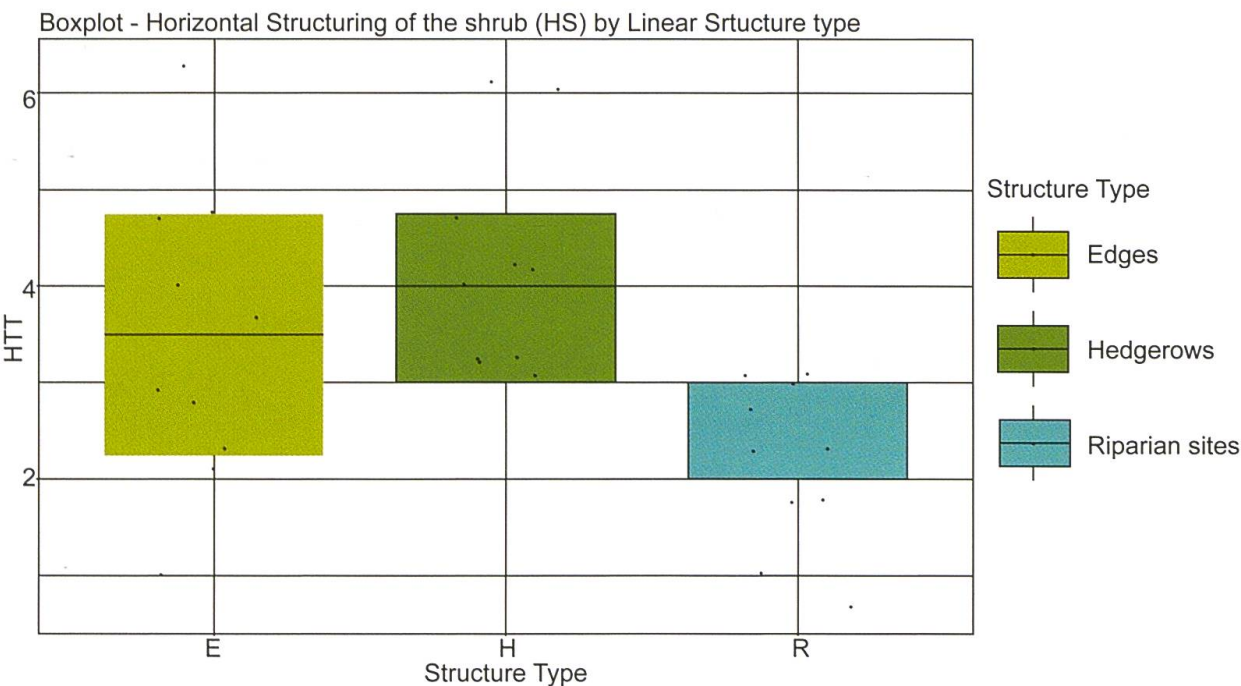
^c Regrouping *P. avium*, *P. mahaleb* and *P. padus* under the functional group of wild cherries may be relevant for the HD because these three species are comparable in their phenology, size, fruits, and leaves, and they often grow in the same areas. However, not all species of the genus *Prunus* were part of the group. Indeed, whereas wild cherries grow on medium-sized trees with average leaves and soft fruits, the blackthorn (*P. spinosa*) is a very thorny bush with small leaves and tougher fruit (BRIGHT *et al.*, 2006; FEDYŃ *et al.*, 2021; LAUBER *et al.*, 2018). We considered the latter species separately.

^d In the UK, *R. canina* provides suitable habitats for the HD. In Switzerland, different species share the same distribution and seasonality, and they are hard to distinguish. Again, these small differences are unlikely to affect the HD. Therefore, to avoid unnecessary fieldwork, we recorded the roses at the genus level (LAUBER *et al.*, 2018).

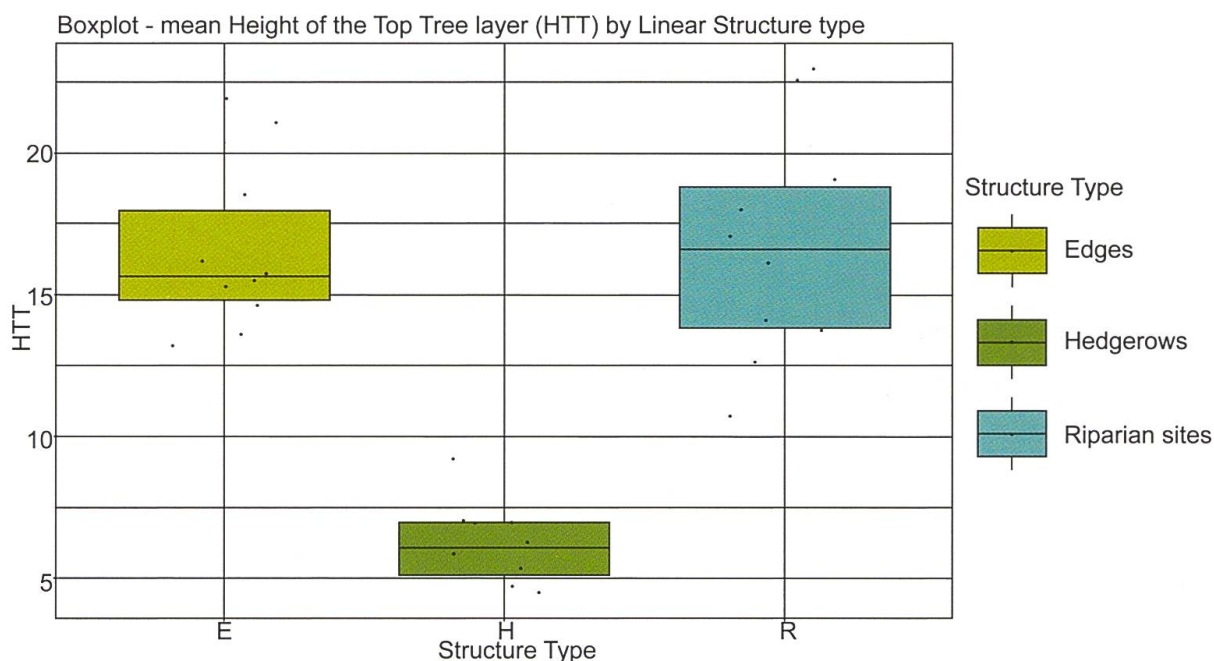
^e We grouped riparian willows (*Salix* spp.) because they all are very similar and regularly form hybrids that are even harder to distinguish for non-specialists. Still, we considered *S. caprea* separately because it differs both ecologically and morphologically from riparian species: it is found in forest-related habitats and has easily recognisable leaves (LAUBER *et al.*, 2018).

^f We considered *S. nigra* and *S. racemosa* together because, besides belonging to the same genus, they also share homologous characters such as odorant flowers and fruits in bunches, and there is overlap in their phenology (LAUBER *et al.*, 2018).

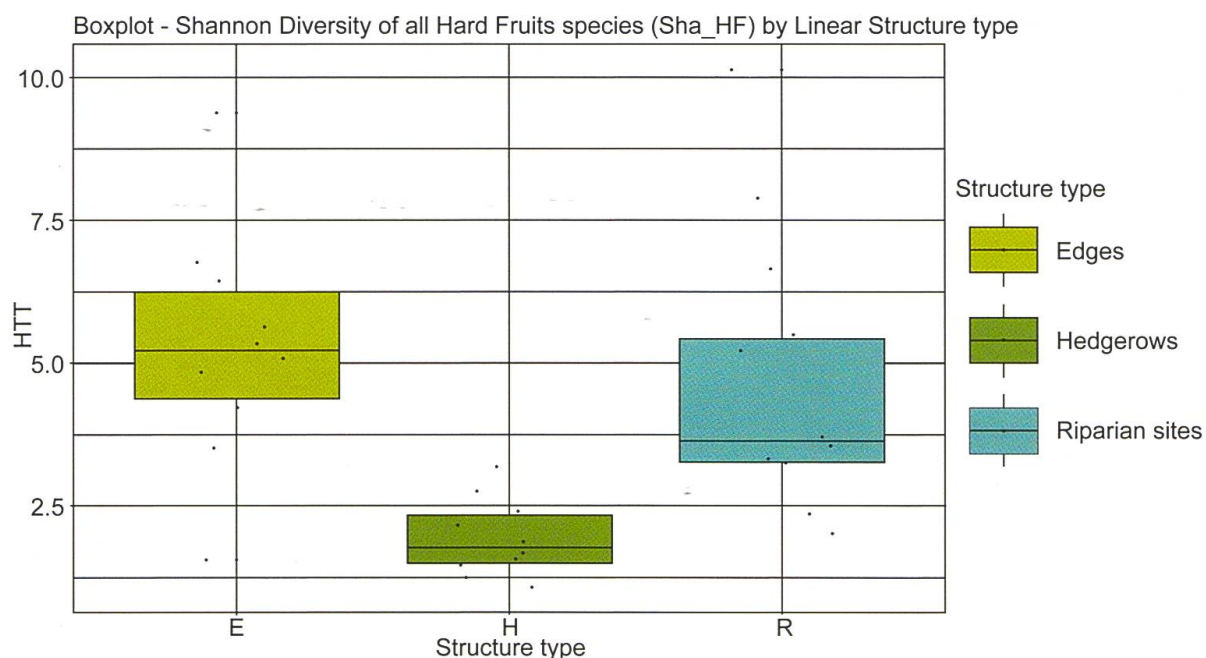
Graph 1. Boxplot of the mean distribution of the horizontal structuring of the shrub by the structure type.



Graph 2. Boxplot of the mean distribution of the mean height of the top tree layer by the structure type.



Graph 3. Boxplot of the mean distribution of the Shannon diversity of hard fruit species by the structure type.



For the sake of brevity, we have only given one example, but a trend like that observed above is found with the other tree-related plant diversity variables (Sp.R_T, Sha_T, Sim_T, Sp.R_HF, Sha_HF, and Sim_HF).

