

**Complementary sampling approaches for woodland beetles,
particularly saproxylic species: Implications for woodland
conservation monitoring**

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Abstract

Saproxylic beetles are declining across Europe due to habitat loss and limited ecological understanding. This highlights the importance of evidence-based sampling strategies for accurately capturing diverse beetle assemblages and supporting baseline inventories and conservation efforts. We present the first European study to simultaneously compare flight-intercept, emergence, and pan traps for sampling woodland beetle abundance, species richness, and assemblage composition. We analysed the entire beetle assemblages and their saproxylic subsets, thereby addressing a conservation-priority group whilst also informing general beetle monitoring. Trap type and design significantly affected capture rates and assemblage composition. Flight-intercept traps collected the greatest abundance and species richness; however, each trapping method sampled distinct assemblage components. Within trap types, pan trap colour and flight-intercept bottle direction further structured assemblages. Blue pan traps captured significantly greater abundances than white and yellow pan traps, and north-facing flight-intercept bottles captured significantly fewer specimens than those facing south and west. Furthermore, flight-intercept and pan trap assemblages were significantly correlated. Our results support the view that multi-method sampling strategies capture complementary components of resulting assemblages, including for saproxylic beetle species. Flight-intercept traps represent an effective core sampling method, while emergence and pan traps further broaden species coverage. However, where resources are limited, pan traps may be omitted, provided flight-intercept traps are retained.

Implications for Insect Conservation

Our findings provide a strong evidence base for improving the taxonomic breadth of saproxylic beetle sampling, supporting baseline inventories, biodiversity assessment, and conservation planning, including the development of tools such as habitat scorecards, national species lists, and Red-List assessments.

Keywords Saproxylic Coleoptera, Woodland Sampling, Trap Efficacy, Sampling Methodology, Biodiversity Monitoring, Evidence-based Conservation.

Introduction

Saproxylic species are those involved in or dependent on dead/decaying wood, the fungal-decay-of-wood process, or its by-products (Speight 1989; updated by Alexander 2008). These species form a substantial proportion of European woodland biodiversity (Siitonen 2001; Stokland et al. 2012; Haeler et al. 2021; Lachat et al. 2025). Coleoptera are the largest insect order (Siitonen 2001; Bouget et al. 2008b; Stokland and Meyke 2008) and provide

important ecological services, including nutrient cycling (Siitonen 2001; Stokland et al. 2012; Ulyshen 2018) and pollination (Gutowski 1990). They also serve as reliable bioindicators of woody-habitat health and management effects (Siitonen 2001; Bouget et al. 2014; Eckelt et al. 2018). Despite their importance, saproxylic beetles remain poorly integrated into woody-habitat assessment frameworks, particularly in Ireland, where baseline data have yet to be translated into conservation-quality statistics for site evaluation and comparison (Alexander and Anderson 2012). Furthermore, European populations are declining due to ongoing tree loss, habitat degradation, and lack of ecological knowledge regarding species status and requirements (Nieto and Alexander 2010; Carpaneto et al. 2015). Thus, further saproxylic beetle research is required, for which effective, targeted sampling strategies are an essential prerequisite.

Saproxylic beetles are difficult to sample due to their taxonomic diversity (Andersson et al. 2014), rarity (Martikainen and Kouki 2003; Martikainen and Kaila 2004), specialised ecologies, cryptic behaviour, and often limited dispersal (Ulyshen 2018; Mendicino et al. 2025). Sampling challenges are further amplified in complex woodland environments, where structural heterogeneity can limit the effectiveness of individual sampling methods (Kitching et al. 2001; Leather 2005; Brockerhoff et al. 2023; Crowley et al. 2023). As such, multi-method sampling approaches, each targeting different woodland microhabitats, are often used to capture a broader range of local beetle taxa (Burner et al. 2022; Crowley et al. 2023). Several studies have compared sampling methods (Wikars et al. 2005; Hyvärinen et al. 2006; Alinvi et al. 2007), with flight-intercept and emergence traps among the most widely used. However, to the best of the authors' knowledge, no previous studies have simultaneously compared flight-intercept, emergence, and pan traps for woodland beetles. Pan traps remain underutilised in saproxylic beetle research, despite their potential to target a distinct component of the beetle assemblage, i.e., flower-visiting (pollinator) taxa. This is surprising given that many saproxylic beetle species, although associated with dead/decaying wood microhabitats as larvae, use floral resources for food and mating purposes as adults (Alexander and Anderson 2012; Duff 2016). These traps may, therefore, capture additional components of the beetle assemblage by capturing taxa linked to different life-history stages and resource use. As such, pan traps were compared with flight-intercept and emergence traps here, to determine their relative effectiveness in saproxylic beetle research. Furthermore, given that flight-intercept traps are the most commonly used sampling method for saproxylic beetles, and are often deployed alone in large-scale site evaluations or monitoring projects (Hyvärinen et al. 2006; Alinvi et al. 2007; Bouget et al. 2008a; Sverdrup-Thygeson and Birkemoe 2009), we evaluated whether these traps serve as a reliable proxy for local beetle assemblages captured by emergence and pan traps. Specifically, we assessed whether flight-intercept traps, when used in isolation, miss key ecological

information. Furthermore, we determined which trap type could be omitted with *minimal* ecological data loss in studies where resource limitations require simplified sampling. Moreover, this study addresses a methodological gap in woodland beetle research by analysing compositional patterns across the entire beetle assemblage, as well as the saproxylic subset (Alinvi et al. 2007). While many studies compare methods across predefined functional guilds (e.g., saproxylic versus non-saproxylic species), such approaches may limit the ability to capture broader patterns in assemblage structure and sampling performance. This is particularly relevant in method-comparison studies, where trap sample assemblages comprise multiple functional guilds, within which saproxylic species form a major ecological subset rather than an isolated group (Grove 2002; Bouget et al. 2008a). Here, we instead analyse data at the level of the sampled assemblage (taxocoenosis), allowing an assessment of overall method effectiveness across the full beetle assemblage before focusing specifically on saproxylic species as a conservation-priority group. This analytical approach enables a comprehensive evaluation of sampling strategies, capturing general ecological patterns, while also revealing responses specific to saproxylic taxa. As such, it provides a valuable basis for informing both targeted saproxylic research and broader woodland beetle biodiversity assessments. Within this wider methodological and ecological context, Ireland's saproxylic beetle fauna provides an especially relevant case study, where targeted monitoring and conservation of these beetles remain particularly limited.

Although historically understudied and mistakenly considered depauperate, recent research shows that Ireland's saproxylic beetle fauna is relatively species-rich, including at least 208 natives and several species of global biogeographic significance (Alexander and Anderson 2012). Many species persist at the westernmost edge of their European ranges and may experience distinct isolation, as well as climatic and habitat pressures. While not yet demonstrated for Irish saproxylic beetles, studies of other range-edge insect populations show that such conditions can alter species dispersal, phenology, and life-history traits (Burton et al. 2010; Clark et al. 2022; Ittonen et al. 2022; Dederichs et al. 2024). Therefore, some Irish saproxylic beetle species may differ ecologically and behaviourally from their British and European counterparts. This potentially distinct fauna survives under conditions of extreme habitat scarcity, however, leaving species increasingly vulnerable. Historical deforestation has reduced Ireland's tree cover to the lowest in Europe (~11%). The majority of this tree cover (~9%) consists of non-native, monocultural conifer plantations (Department of Agriculture, Food and the Marine 2023), which are typically known to support lower invertebrate biodiversity and reduced abundance of woodland specialist taxa (Fahy and Gormally 1998; Fuller et al. 2008). Only ~2% of Ireland's tree cover comprises native woodland (Bullock et al. 2014) which, in comparison to plantations, supports higher biodiversity and provides a diversity of

woody microhabitats essential for saproxylic beetle survival (Grove 2002; Stokland et al. 2012). These woodlands include important old-growth habitats, such as ancient woodlands, which are scarce, fragmented, and threatened in Ireland. Notably, 50% of native Irish saproxylic beetle species are considered rare, which likely reflects this habitat scarcity and Ireland's island biogeography. This emphasises the fragility of Ireland's fauna (Hall 1995; Mitchell 1995; Rackham 1995; Perrin and Daly 2010; Alexander and Anderson 2012; Bullock et al. 2014; FOREST EUROPE 2020) and the habitats they depend on. As such, there is a clear need to document the beetle assemblages supported by these remaining native woodlands, thereby establishing robust faunistic baselines, quantifying their biodiversity value, and informing effective conservation management strategies for saproxylic species. Importantly, understanding these Irish assemblages may also have broader European relevance. As an island with the lowest European tree cover, Ireland provides a benchmark for understanding how saproxylic beetle assemblages respond to sustained habitat fragmentation and loss. Ireland's fauna, already isolated from British and European sources, has populations further separated within the island by the extreme patchiness of native woodland (Perrin and Daly 2010; Alexander and Anderson 2012), creating a double pressure that increases their vulnerability. More broadly, the Irish fauna may provide internationally valuable insights: both as a reference for how woodland invertebrate communities elsewhere may decline, if native tree habitats continue to be lost; and as an urgent warning for conservation action. However, realising this potential depends on the ability to accurately sample and document the poorly described Irish fauna. As such, robust comparative methodological studies are necessary to determine the relative effectiveness of different sampling methods for these beetle assemblages.

Therefore, we present the first Irish study to compare trapping methods for saproxylic species, and the first European study to compare flight-intercept, emergence, and pan traps within a single integrated sampling design. We assessed trap performance at the level of the full beetle assemblage, alongside the saproxylic subset, allowing us to assess overall sampling effectiveness, while also addressing a group of conservation concern. Our specific research questions were to:

1. Compare the effectiveness of flight-intercept, emergence, and pan traps for sampling beetle abundance, species richness, and assemblage composition.
2. Assess the influence of a) pan bowl colour, and b) flight-intercept bottle direction, on beetle abundance, species richness, and assemblage composition.

3. Investigate whether flight-intercept traps serve as a reliable proxy for beetle assemblages captured by emergence and pan traps.

Materials and Methods

Study Area

The study was conducted at St John's Wood (Lough Ree SAC (000440); SPA (004064)), located in the Irish midlands (Lat: 53.5523, Long: -8.0040, Fig. 1). The site is one of Ireland's largest ancient woodlands (110ha) and almost 20% of Ireland's saproxylic invertebrate species have been recorded here, including rare, old-growth relic Coleoptera (Rackham 1995; Perrin et al. 2006; Perrin and Daly 2010; Alexander 2011). The woodland is classified as a coppice-with-standards and comprises a mixture of *Quercus robur* L. (Fagaceae), *Fraxinus excelsior* L. (Oleaceae), *Corylus avellana* L. (Betulaceae), *Salix cinerea* L. (Salicaceae), and *Alnus glutinosa* (L.) Gaertn. (Betulaceae) (Perrin et al. 2006). The wood is bordered to the south by pasture and wetlands, and to the north, east, and west by Lough Ree. The bedrock is limestone (Parkes et al. 2012) with an undulating topography composed of sandy and acid clays, overlaying a subsoil of predominantly limestone till, karst, and peat (Rackham 1995; EPA 2018). Site elevation is ~47m, mean annual precipitation is ~1,014mm, and average minimum and maximum temperatures are 6°C and 13°C, respectively (Met Éireann n.d. a). Extensive winter flooding occurs in areas along Lough Ree and the peatlands (Alexander 2011; OPW n.d.). The woodland has had a complex history of ownership and management. Currently, most of the woodland (70%) is owned by the National Parks and Wildlife Service and is managed for biodiversity. Livestock are excluded, and the lack of natural grazing has led to the development of a thick field and shrub layer of *Ilex aquifolium* L. (Aquifoliaceae) and *Hedera helix* L. (Araliaceae).

Sampling Strategy

Eighteen veteran *Q. robur* trees were randomly selected as focal trees (FTs) across the woodland (Fig. 1). All FTs were categorised as "veteran" using a specifically designed scorecard (Online Resource 1: Table S1) and were >50m apart to provide trap independence and reduce spatial autocorrelation (Buse et al. 2008; Parmain et al. 2013; Allison et al. 2014; Burner et al. 2022). At each FT, three methods (Fig. 2) were used to trap beetles, each targeting different woodland strata, i.e., ground layer, field layer, and shrub layer: 1) A flight-intercept trap (IT) collected beetles in flight using the shrub layer (Carrel 2002; Alexander 2011; Alexander et al. 2014). One IT was positioned on a southern-facing branch of each FT, 1.5m above ground and 30cm from the tree trunk. A standardised height

of 1.5m was chosen to ensure consistency with previous woodland beetle studies (Alexander 2011; Bouget et al. 2013; Parmain et al. 2013; Janssen et al. 2017), while also facilitating safe and efficient trap deployment and repeated sampling under dense understory and uneven terrain. Individual ITs consisted of four upturned bottles, each with a surface opening oriented towards one of the cardinal directions (N, E, S, W), through which flying beetles were intercepted and collected (Fig. 3). As such, four directional subsamples were collected from each individual trap. 2) A pan trap (PT) (Campbell and Hanula 2007; Vrdoljak and Samways 2012; Crowley et al. 2023) was placed in a pocket of light, 10m east of each FT, and collected beetles using the field layer. Each PT consisted of three coloured bowls (blue, white, and yellow). Thus, three separate subsamples were collected from each individual trap. 3) An emergence trap (ET) (Ferro and Carlton 2011; Lee et al. 2014; Macagno et al. 2015) collected beetles emerging directly from dead/decaying wood and was deployed in the shade just north of each FT.

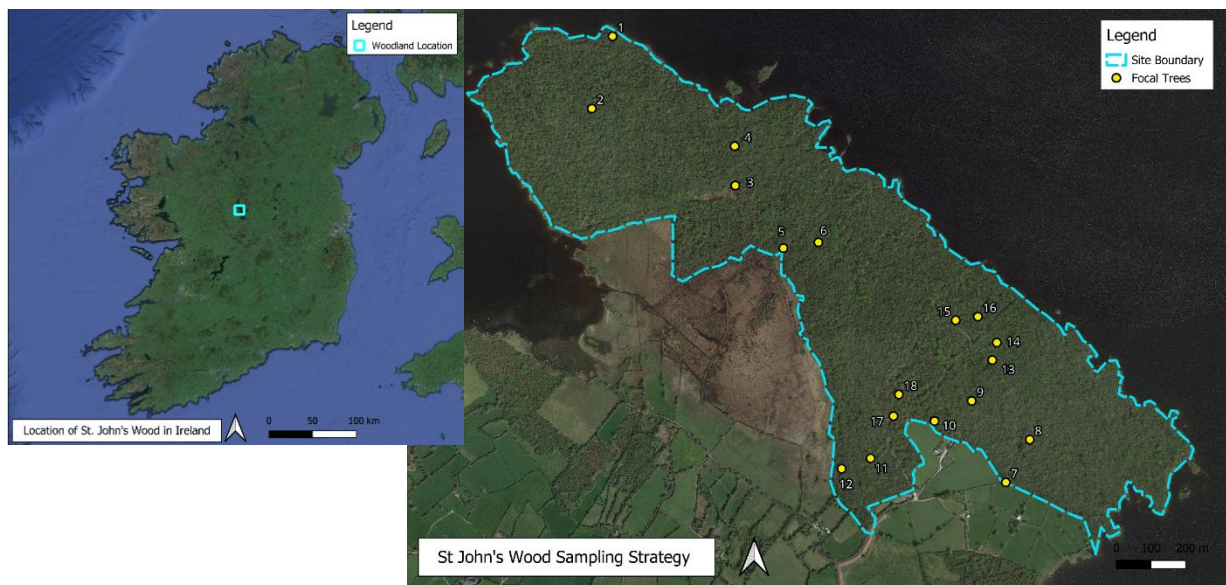


Fig. 1 Location of St John's Wood in Co. Roscommon, within the Irish midlands (Left). Sampling strategy showing the woodland boundary in a blue hatched line, and the 18 randomly selected sampling locations (focal trees - veteran *Quercus robur* L. (Fagaceae)) in yellow dots (Right). A Crowe 2025, QGIS



Fig. 2 Trap set-up at each focal tree (sampling location), illustrating the relative positions of flight-intercept, emergence, and pan traps

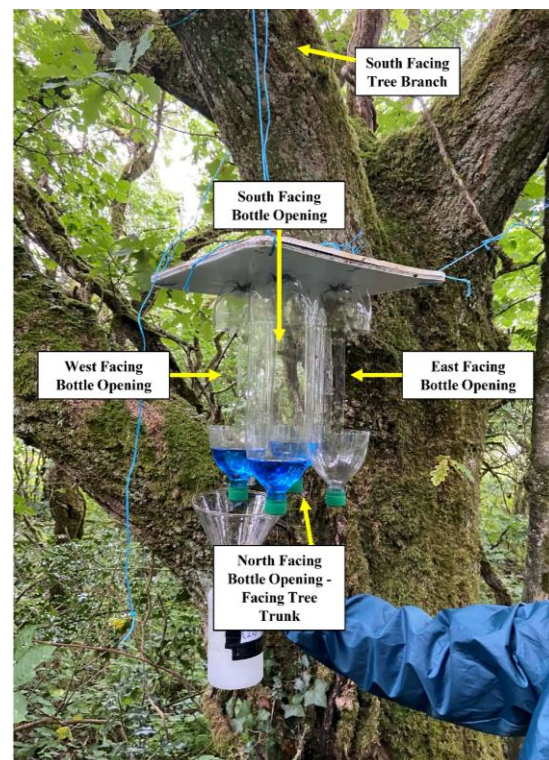
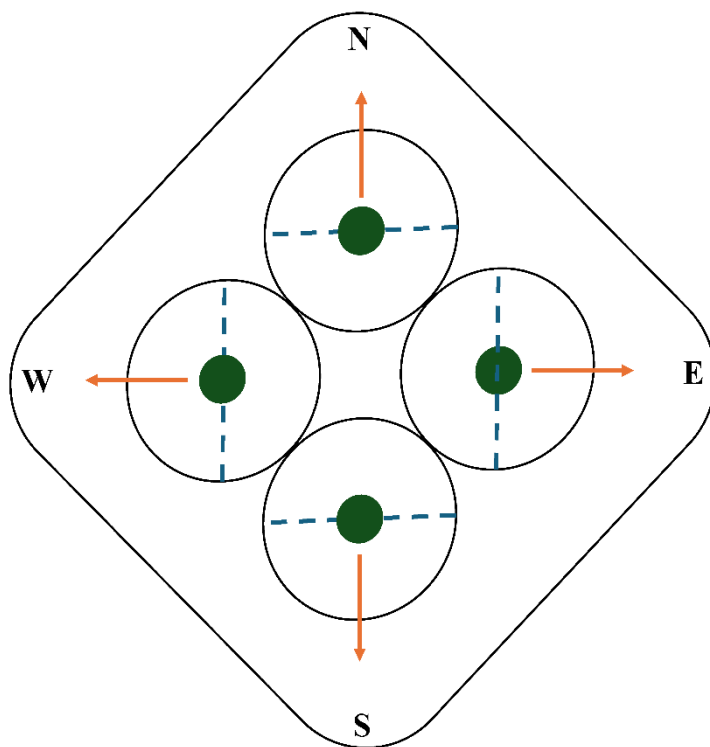


Fig. 3 Schematic of a flight-intercept trap (left), showing a top-down view of the trap. Large circles represent the four upturned bottles, while the small green circles represent their lids. Blue dashed lines indicate the opening cut into each bottle, and orange arrows show the orientation of each opening in the cardinal directions (N, E, S, W). The image (right) shows a trap suspended from a south-facing tree branch, and again illustrates the orientation of the four bottle openings

Each ET contained an equal weight of fresh and advanced decayed deadwood (Table 1), randomly collected from the woodland floor within a 20m radius of each FT (Online Resource 1: Figs S1-S3 for detailed trap information).

Table 1 Deadwood categories used to classify dead/decaying wood sampled in each of the 18 emergence traps

Deadwood Category	Features
Fresh Deadwood	Dead 1-2 years. Substrate still firm, no peeling bark, no insect holes present, wood still sound and often twigs attached.
Advanced Decay	Dead >2 years. Evidence of decay, peeling and missing bark, soft wood, insect holes present, bark can be torn apart using fingers or knife, wood falling apart, substrate losing original shape.

Deadwood categories were based on wood condition and level of decay. The criteria used to classify each deadwood category were based on, and modified from, Irmiler et al. (1996), Jonsell et al. (1998), Fayt et al. (2006), Gibb et al. (2006), and Lachat et al. (2006). Deadwood classifications were made in the field by the author during the trap-set-up process

Fortnightly samples (June – September, 2022) were collected from ITs and ETs. The PTs were set up for five days during calm/sunny weather, once in July, August, and September (2022). Staphylinidae were identified to species level by Dr. Jervis Good. Remaining families were identified to species level by the first author following Unwin (1984), Luff (2007), Duff (2012, 2016, 2020), Hackston (n.d.), and with reference to the entomological collections at the National Museum of Ireland – Natural History. Dr. Keith Alexander (Freelance Ecological Consultant, Truro, UK) also confirmed six specimens. Voucher specimens have been deposited in the National Museum of Ireland – Natural History, to ensure the long-term storage and availability of these valuable taxonomic, biogeographical, and temporal distribution data.

Data Analysis

Statistical analyses were conducted using beetles identified to species level. Beetle data were categorised into two groups: 1) “All Beetles” (all species combined, including known saproxylic taxa); and 2) “Saproxylic” (only known saproxylic species included). Analyses were conducted separately for each group, allowing patterns to be assessed across the full Coleopteran assemblage, before focusing on the saproxylic subset. This approach allowed overall sampling method performance to be assessed across the full beetle assemblage, while also evaluating how effectively the methods captured saproxylic species. For the purposes of this paper, beetle species that adhered to the following criteria (Table 2) were classified as saproxylic or not saproxylic, i.e., other woodland-associated beetles.

215 **Table 2** Classifications of saproxylic versus non-saproxylic beetle species (Crowe et al. in prep.):

Classification	Criteria
Species were classified as saproxylic if they met one or more of the following criteria	Feed directly on dead/decaying wood or products of wood decay, e.g., wood fungi/wood mould. Have immature stages (includes larvae) that develop in: dead/decaying wood (includes woody plant stems, e.g., dead/decaying <i>H. helix</i>); or in the products of wood decay e.g. wood fungi. Use the following saproxylic microhabitats - tree cavities, rot-holes, wood mould, animal nests in trees made of dead/decaying wood, tree sap.
Species were classified as non-saproxylic if they met one or more of the following criteria	Have no known ecological associations currently with dead/decaying wood, the process of the fungal decay of wood or the products of that decay, or the saproxylic microhabitats noted above. Lack sufficient, reliable ecological information currently to make an informed decision that the species is saproxylic. Feed directly on live wood, e.g., live tree roots. Are considered opportunistic users of wood for shelter/predation ground, e.g., predators/scavengers, where there is no evidence to prove that dead/decaying wood is used for immature stage development.

216 Criteria were informed by, but not limited to, detail in the Irish and British saproxylic beetle/invertebrate annotated
217 checklists, i.e., knowledge base for Irish fauna (Alexander 2002; Alexander and Anderson 2012). Classifications
218 are based on current ecological knowledge and may be refined as further information becomes available, or as
219 definitions of saproxylic species evolve. A distinction between obligate and facultative saproxylic species was not
220 applied, as such distinctions could not be accurately and consistently applied given limited ecological information
221 available on many taxa, specifically regarding larval ecology and degree of substrate dependence. As the Irish
222 saproxylic fauna is currently understudied, there is a particular paucity of ecological information for many taxa,
223 meaning evidence required to confidently determine the dependence of a species upon saproxylic habitat is
224 lacking. Furthermore, species ecology can vary across regions, meaning that obligate classifications derived from
225 other geographic contexts should not be applied directly to Irish populations without reliable evidence supporting
226 such an association level. For these reasons, a broader evidence-based approach was adopted here, whereby
227 species were classified as saproxylic based on reliable evidence of ecological association with dead/decaying
228 wood; wood-decay by-products; or related wood-decay microhabitats. This approach provides ecologically
229 informed species groupings and is broadly consistent with the categorisation of beetles in wider European beetle
230 assessments (Nieto and Alexander 2010; Carpaneto et al. 2015)

231 Prior to all statistical analyses, beetle data across the eight sampling sessions were pooled within each trap
232 configuration (i.e., Trap Type, PT Colour, and IT Direction) to generate single cumulative abundance, species

richness, and composition datasets for each trap sample. This removed dependence associated with repeated temporal sampling, ensuring that analyses were conducted on cumulative trap-level samples rather than repeated collection-period observations. To determine the effects of: 1) Trap Type; 2a) PT Bowl Colour; and 2b) IT Bottle Direction, on beetle abundance and species richness, Generalized Linear Models (GLMs) were run using IBM SPSS Statistics (v29.0.2.0) (IBM Corp 2023). Model distributions were selected based on optimal fit for each dataset, as determined by goodness-of-fit criteria (Online Resource 2). Across all GLMs, FT was included as an additional fixed blocking factor alongside the primary explanatory variable (Trap Type, PT Colour, or IT Direction) to account for non-independence among samples originating from the same sampling location. When analysing Trap Type effects, data were grouped by FT and Trap Type, i.e., pooled colours for PTs and directions for ITs, to allow for broad comparisons of trap efficacies. Data were further split by PT Colour and IT Direction when testing for these effects. When testing for Trap Type effects, analyses were performed using both raw data and data adjusted for sampling effort. This accounted for unequal sampling intensity between trap types (PTs vs ITs and ETs), allowing for a fair comparison of trap effectiveness. To determine the effects of: 1) Trap Type; 2a&b) PT Colour and IT Direction, on beetle assemblage composition, multivariate analyses were carried out using PC-ORD (v6) (McCune and Grace 2002; McCune and Mefford 2011). To account for differences in sampling effort across Trap Type, and to standardise abundance data across traps, species data was relativised by trap totals (row). Non-metric Multidimensional Scaling (NMS) and Principal Coordinates Analysis (PCoA) were conducted to identify and explore multivariate patterns in species composition. Multi-response Permutation Procedures (MRPP) tested for statistically significant differences in species composition between groups. Where MRPP analyses indicated significant differences among groups, homogeneity of multivariate dispersions (PERMDISP) was assessed using Bray–Curtis distances calculated from row-relativised species data in R (Vegan Package; Oksanen et al. 2024; R Core Team 2025). These analyses determined whether patterns were also influenced by variation in dispersion, rather than reflecting compositional differences among group centroids alone. To assess potential sampling-location effects within multivariate datasets, additional PCoA and MRPP (where permitted by data structure) analyses were conducted using FT as the grouping variable. Indicator Species Analysis (ISA) was conducted using un-relativised species data (as ISA internally standardises species abundance and frequency data during calculations), and identified species that had statistically significant associations with specific groups (Dufrêne and Legendre 1997). To assess correlations between the IT beetle assemblage and the other trap type assemblages, Mantel tests were run on PC-ORD, using species data that was relativised by trap totals and fourth-

root transformed (useful for balancing moderately skewed data by reducing the influence of dominant species, while preserving rare species). The value of significance for all tests was set at <0.05 .

Results

A total of 1,937 beetle specimens were collected (1,923 identified to species level, with remaining 14 unidentifiable due to damage), totalling 32 families and 163 species. Most specimens identified belonged to the Staphylinidae (54%), followed by Cryptophagidae (9%) and Latridiidae (6%). Staphylinidae also represented the greatest species richness ($n=51$ species), followed by Curculionidae ($n=20$ species), and Nitidulidae and Ptiliidae (both $n=8$ species). The staphylinid, *Eusphalerum luteum* (Marshall, 1802), represented 42% of the total catch, followed by *Cryptophagus scanicus* (Linnaeus, 1758) (Cryptophagidae) and *Cartodere nodifer* (Westwood, 1839) (Latridiidae) at 5% and 4% respectively. As mentioned, beetle data was split into two groups for statistical analyses: 1) “All Beetles” consisting of all beetle species found; 2) “Saproxylis” consisting of only a subset of the species found, which were saproxylis in nature. Saproxylis beetles formed a substantial component of the overall beetle assemblage, accounting for 55% of the total species and 43% of all specimens found. Furthermore, saproxylis species were present in 22 of the 32 families recorded.

1) Effect of Trap Type:

Abundance/Species Richness

Trap Type (adjusted for sampling effort) significantly affected the abundance and species richness of both beetle groups, when tested separately ($p < 0.001$). For both response variables, pairwise comparisons revealed consistent patterns across both beetle groups. Regarding abundance, ITs had significantly greater abundance than both ETs and PTs ($p < 0.001$ for both beetle groups), while ETs had significantly lower abundance than PTs ($p < 0.001$ for both beetle groups). Regarding species richness, ITs had significantly greater species richness than ETs ($p < 0.001$ for both beetle groups) and PTs (“All Beetles”: $p = 0.005$; “Saproxylis”: $p = 0.011$), while ETs had significantly lower species richness than PTs ($p < 0.001$ for both beetle groups) (Online Resource 2).

Beetle Assemblage Composition

Across both beetle groups, ITs captured the greatest overall species richness, followed by ETs and PTs (“All Beetles”: ITs = 118, ETs = 51, PTs = 46; “Saproxylis”: ITs = 66, ETs = 32, PTs = 26). Furthermore, Venn diagrams show that across both beetle groups, each trap type captured unique species with relatively limited overlap (Online Resource 1: Figs S4-S5). For the “All Beetles” group, ITs recorded 75, ETs 25, and PTs 17 unique species. For

the “Saproxylic” group, ITs recorded 36, ETs 15, and PTs 7 unique species. Flight-intercept traps recorded the highest proportion of unique captures (species and specimens, i.e., species occurring in a single trap type, and the total number of specimens belonging to those species), followed by ETs and PTs (Table 3).

Table 3 Proportion of unique species and specimens captured across the three trap types: flight-intercept (IT); emergence (ET); and pan (PT) traps. Values are shown for both beetle groups (“All Beetles” – Includes all beetle species found; “Saproxylic” – Subset of the “All Beetles” group including only saproxylic beetle species found)

Trap Type	“All Beetles” Unique Species	“All Beetles” Unique Specimens	“Saproxylic” Unique Species	“Saproxylic” Unique Specimens
IT	46%	20%	40%	33%
ET	15%	3%	17%	4%
PT	10%	1%	8%	2%

Unique species are those species occurring in a single trap type (expressed as a percentage of total species). Unique specimens are the total number of beetle specimens belonging to these unique species

The PCoA tests (unimodal response data, Sørensen [Bray-Curtis] distance measure) found that the first three axes of the “All Beetles” group explained a meaningful portion of the variance (Corrected Cumulative %Variance: Axis 1 = 12.678, 2 = 22.704, 3 = 31.435). A randomisation test (999 permutations) confirmed that Axes 1-3 were statistically significant ($p = 0.001$). The ordination plot (Fig. 4) shows substantial separation between beetle assemblages across trap types, with minimal overlap between convex hulls. The first two axes of the “Saproxylic” group also explained a meaningful portion of the variance (Corrected cumulative %Variance: Axis 1 = 12.221, 2 = 22.115). A randomisation test (999 permutations) confirmed that both axes were statistically significant ($p = 0.001$). The ordination plot (Fig. 4) showed strong compositional differentiation among trap type assemblages, with no overlap between convex hulls.

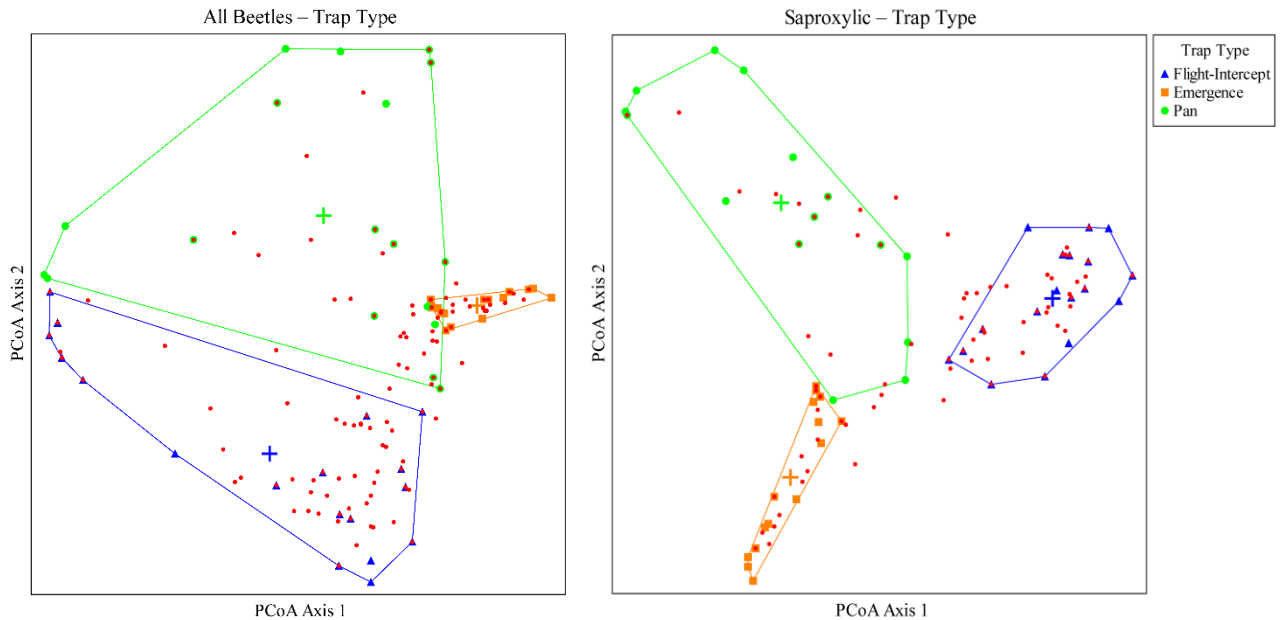


Fig. 4 Principal Coordinates Analysis (PCoA) ordination plots of beetle assemblage composition sampled across each of the three trap types: blue triangles represent flight-intercept traps; orange squares represent emergence traps; and green circles represent pan traps. Red dots represent the positioning of beetle species across ordination space. Coloured convex hulls (polygons) outline beetle species associated with each trap type, while coloured crosses indicate group centroids (multivariate means) for each trap category. Ordination plot on the left shows results for the “All Beetles” group, while the plot on the right shows results for the “Saproxylic” group

Differences in beetle assemblages across Trap Type were statistically confirmed by MRPP tests (“All Beetles”: $p < 0.001$, $A = 0.084$; “Saproxylic”: $p < 0.001$, $A = 0.120$). PERMDISP results differed significantly among trap types for both beetle groups (“All Beetles”: $F = 4.465$, $p = 0.014$; “Saproxylic”: $F = 6.278$, $p = 0.006$). Additional PCoA and MRPP analyses assessing FT effects found no clear clustering of assemblages within either beetle group (MRPP - “All Beetles”: $p = 0.375$, $A = 0.005$; “Saproxylic”: $p = 0.994$, $A = -0.046$), indicating that observed Trap Type patterns were not driven by sampling-location effects. Species that had significant associations with specific trap types were identified using ISA tests (Monte Carlo test - 4,999 permutations). The randomisation test for the sum of maximum indicator values (IVmax) was significant for both groups ($p < 0.001$), confirming that species associations with Trap Type were not due to random chance. All species that were significant indicators in the “Saproxylic” dataset were also significant in the “All Beetles” dataset. As indicator values for significant species varied between the two groups, results for both are provided (Table 4).

Table 4 Species Indicator Analysis showing species with statistically significant associations with trap types: flight-intercept (IT); emergence (ET); and pan (PT) traps. "All Beetles" group values are noted in the superscript "ab" columns, while the "Saproxylic" group values are noted in the superscript "s" columns

Species	Trap Type	Indicator ^{ab} Value	Indication ^{ab} Level	<i>p</i> Value ^{ab}	Indicator ^s Value	Indication ^s Level	<i>p</i> Value ^s
<i>Atheta harwoodi</i> B.S. Williams, 1930	IT	27.8	Moderate	0.0096	27.8	Moderate	0.0086*
<i>Agaricochara latissima</i> (Stephens, 1832)	PT	57.2	Strong	0.0002	60.7*	Strong	0.0002
<i>Anaspis maculata</i> Geoffroy, 1785	IT	26.7	Moderate	0.0106	26.6*	Moderate	0.0108*
<i>Anaspis rufilabris</i> (Gyllenhal, 1827)	IT	52.0	Strong	0.0006	51.8*	Strong	0.0004*
<i>Aleochara sparsa</i> Heer, 1839	IT	38.9	Moderate	0.0004	38.9	Moderate	0.0010*
<i>Biblopectus pusillus</i> (Denny, 1825)	IT	22.2	Moderate	0.0292	N/A	N/A	N/A
<i>Byturus tomentosus</i> (De Geer, 1774)	IT	25.6	Moderate	0.0194	N/A	N/A	N/A
<i>Baeocrara variolosa</i> (Mulsant & Rey, 1861)	IT	22.2	Moderate	0.0310	22.2	Moderate	0.0246*
<i>Cychramus luteus</i> (Fabricius, 1787)	IT	38.9	Moderate	0.0012	38.9	Moderate	0.0008*
<i>Cyphon padi</i> (Linnaeus, 1758)	IT	38.9	Moderate	0.0006	N/A	N/A	N/A
<i>Dinaraea aequata</i> (Erichson, 1837)	ET	40.0	Strong	0.0002	40.0	Strong	0.0006*
<i>Epuraea biguttata</i> (Thunberg, 1784)	IT	35.6	Moderate	0.0014	35.5*	Moderate	0.0020*
<i>Enicmus testaceus</i> (Stephens, 1830)	IT	53.0	Strong	0.0002	52.6*	Strong	0.0002
<i>Grynobius planus</i> (Fabricius, 1787)	IT	41.2	Strong	0.0036	41.2	Strong	0.0010*
<i>Grammoptera ruficornis</i> (Fabricius, 1781)	IT	29.2	Moderate	0.0078	29.0*	Moderate	0.0066*
<i>Haploglossa villosula</i> (Stephens, 1832)	IT	61.1	Strong	0.0002	N/A	N/A	N/A
<i>Ocys harpaloides</i> (Audinet-Serville, 1821)	ET	25.4	Moderate	0.0172	25.4	Moderate	0.0148*
<i>Pogonocherus hispidulus</i> (Piller & Mitterpacher, 1783)	ET	26.4	Moderate	0.0264	24.6*	Moderate	0.0174*
<i>Ptenidium nitidum</i> (Heer, 1841)	IT	29.2	Moderate	0.0084	N/A	N/A	N/A
<i>Stenichnus bicolor</i> (Denny, 1825)	IT	61.3	Strong	0.0002	61.0*	Strong	0.0002
<i>Sericoderus brevicornis</i> Matthews, 1890	IT	47.2	Strong	0.0004	47.1*	Strong	0.0008*
<i>Sepedophilus nigripennis</i> (Stephens, 1832)	ET	20.0	Weak	0.0252	N/A	N/A	N/A
<i>Salpingus planirostris</i> (Fabricius, 1787)	IT	36.2	Moderate	0.0012	36.2	Moderate	0.0014*
<i>Salpingus ruficollis</i> (Linnaeus, 1761)	IT	33.3	Moderate	0.0022	33.3	Moderate	0.0028*

In the "Saproxylic" columns,* denotes values that differ from corresponding columns in the "All Beetles" group (for species found in both groups)

2a) Effect of PT Bowl Colour:

Abundance/Species Richness

Pan Trap Colour significantly affected the abundance of both beetle groups ($p < 0.001$). Blue bowls had significantly greater abundance than white and yellow bowls ($p < 0.001$ for both groups). Colour did not significantly affect the species richness for either group (Online Resource 2).

Beetle Assemblage Composition

For the "All Beetles" group, blue and yellow PTs captured the greatest species richness (21 species each), followed by white PTs (18). In contrast, for the "Saproxylic" group, blue PTs captured the greatest species richness (14),

followed by white (11) and yellow PTs (10). Furthermore, across both groups, all PT colours had unique species (Online Resource 1: Figs S6-S7). For the “All Beetles” group, blue bowls recorded 15, yellow bowls 11, and white bowls 10 unique species. For the “Saproxylic” group, blue bowls recorded 9, white bowls 7, and yellow bowls 4 unique species. Overall, blue bowls contributed the highest proportion of unique captures for both beetle groups. Yellow bowls contributed more unique captures than white for the “All Beetles” group, while white bowls contributed more for the “Saproxylic” group (Table 5).

Table 5 Proportion of unique species and specimens captured across the three pan trap bowl colours: blue; white; and yellow, relative to the total pan trap catch

Pan Bowl Colour	“All Beetles” Unique Species	“All Beetles” Unique Specimens	“Saproxylic” Unique Species	“Saproxylic” Unique Specimens
Blue	33%	18%	35%	23%
White	24%	12%	27%	9%
Yellow	22%	7%	15%	13%

Unique species are those species occurring in a pan bowl colour (expressed as a percentage of total species).

Unique specimens are the total number of beetle specimens belonging to these unique species

The PCoA results showed that the first three axes of the “All Beetles” group explained a meaningful portion of the variance in species composition (Corrected cumulative % variance: Axis 1 = 14.492, Axis 2 = 25.548, Axis 3 = 33.715). The ordination plot (Fig. 5) shows partial overlap between all three PT colours. The first two axes of the “Saproxylic” group explained a meaningful portion of the data variation (Corrected cumulative % variance Axis 1: 20.639, Axis 2: 32.123). Overlap is noted between all three PT colours in the ordination plot (Fig. 5). Randomisation tests were not included for either group due to data constraints. However, consistent patterns were observed across analyses. Therefore, PCoA results were considered valid and ecologically informative.

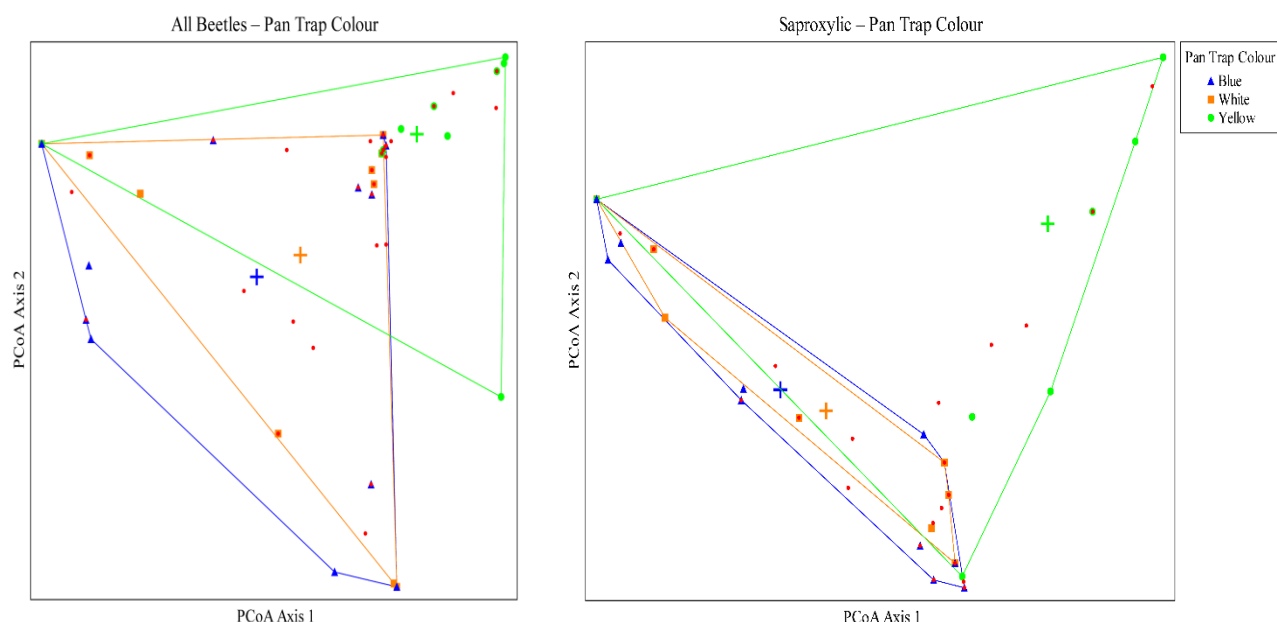


Fig. 5 Principal Coordinates Analysis (PCoA) ordination plots of beetle assemblage composition sampled across each of the three pan trap colours: blue triangles represent blue pan trap bowls; orange squares represent white pan trap bowls; and green circles represent yellow pan trap bowls. Red dots represent the positioning of beetle species across ordination space. Coloured convex hulls (polygons) outline beetle species associated with each pan trap colour, while coloured crosses indicate group centroids (multivariate means) for each colour category. Ordination plot on the left shows results for the “All Beetles” group, while the plot on the right shows results for the “Saproxylic” group

The MRPP results statistically confirmed the above differences (“All Beetles”: $p = 0.001$, $A = 0.040$; “Saproxylic”: $p < 0.001$, $A = 0.092$). PERMDISP values did not differ significantly among PT colours for either beetle group (“All Beetles”: $F = 0.0454$, $p = 0.641$; “Saproxylic”: $F = 0.298$, $p = 0.731$). Additional PCoA ordinations with samples grouped by FT showed no strong or consistent clustering of PT assemblages across either beetle group, although some tree-specific variation was evident. The ISA results revealed species strongly associated with each colour (Table 6) and randomisation tests for the sum of IVmax were significant for both groups ($p < 0.001$). All species that were significant indicators in the “Saproxylic” dataset were also significant in the “All Beetles” dataset, with the exception of *Grynobius planus* (Fabricius, 1787) (Ptinidae) which was non-significant in the “All Beetles” dataset ($p = 0.078$).

Table 6 Species Indicator Analysis results showing species with statistically significant associations with different pan trap bowl colours: blue; white; and yellow. "All Beetles" group values are noted in the superscript "ab" columns, while the "Saproxylic" group values are noted in the superscript "s" columns

Species	Pan Bowl Colour	Indicator ^{ab} Value	Indication ^{ab} Level	<i>p</i> Value ^{ab}	Indicator ^s Value	Indication ^s Level	<i>p</i> Value ^s
<i>Agaricohara latissima</i> (Stephens, 1832)	Blue	34.6	Moderate	0.0392	N/A	N/A	N/A
<i>Bibloporus bicolor</i> (Denny, 1825)	Blue	23.5	Moderate	0.0294	N/A	N/A	N/A
<i>Cartodere nodifer</i> (Westwood, 1839)	Yellow	57.1	Strong	0.0002	66.7*	Strong	0.0002
<i>Gyrohaena minima</i> (Erichson, 1837)	White	19.8	Weak	0.0788	27.2	Moderate	0.0354

In "Saproxylic" columns, * denotes values that differ from corresponding columns in the "All Beetles" group (for species found in both groups)

2b) Effect of IT Bottle Direction:

Abundance/Species Richness

Flight-intercept Bottle Direction had a significant effect on "All Beetles" abundance only ($p = 0.026$). North-facing bottles had significantly lower abundance than south ($p = 0.001$) and west-facing bottles ($p = 0.020$). Direction did not significantly affect the species richness of either group (Online Resource 2).

Beetle Assemblage Composition

Across both beetle groups, east-facing IT bottles captured the greatest overall species richness ("All Beetles" = 60 species; "Saproxylic" = 40 species). For the "All Beetles" group, north and south-facing bottles each captured 58 species, while west-facing bottles captured 57 species. For the "Saproxylic" group, south-facing bottles captured 35 species, followed by north-facing (34 species) and west-facing bottles (32 species). Furthermore, across both groups, all IT directions had unique species (Online Resource 1: Figs S8-S9). For the "All Beetles" group, east-facing bottles recorded 18, south-facing bottles 16, north-facing bottles 14, and west-facing bottles 11 unique species. For the "Saproxylic" group, east-facing bottles recorded 13, south-facing bottles 7, north-facing bottles 6, and west-facing bottles 5 unique species. Overall, east bottles contributed the highest proportion of unique captures. South and north bottles captured a moderate share of unique captures, while west bottles contributed the lowest (Table 7).

Table 7 Proportion of unique species and specimens captured across flight-intercept bottle directions: north; east; south; and west, relative to the total flight-intercept trap catch

Intercept Bottle Direction	“All Beetles” Unique Species	“All Beetles” Unique Specimens	“Saproxyllic” Unique Species	“Saproxyllic” Unique Specimens
North	12%	1%	9%	1%
East	15%	1%	20%	2%
South	14%	1%	11%	1%
West	9%	1%	8%	1%

Unique species are those species occurring in a flight-intercept bottle direction (expressed as a percentage of total species). Unique specimens are the total number of beetle specimens belonging to these unique species

The PCoA results showed that the first three axes of the “All Beetles” group explained a meaningful portion of the variance in species composition (Corrected cumulative % variance: Axis 1 = 17.649, Axis 2 = 27.051, Axis 3 = 34.300). The plot (Fig. 6) shows minimal compositional differences in beetle assemblages across direction, with considerable overlap evident. A relatively low variance was explained by the first two axes for the “Saproxyllic” group (Corrected cumulative % variance: Axis 1 = 9.246, Axis 2 = 17.551). The plot (Fig. 6) shows some separation between IT directions, however, there is substantial overlap.

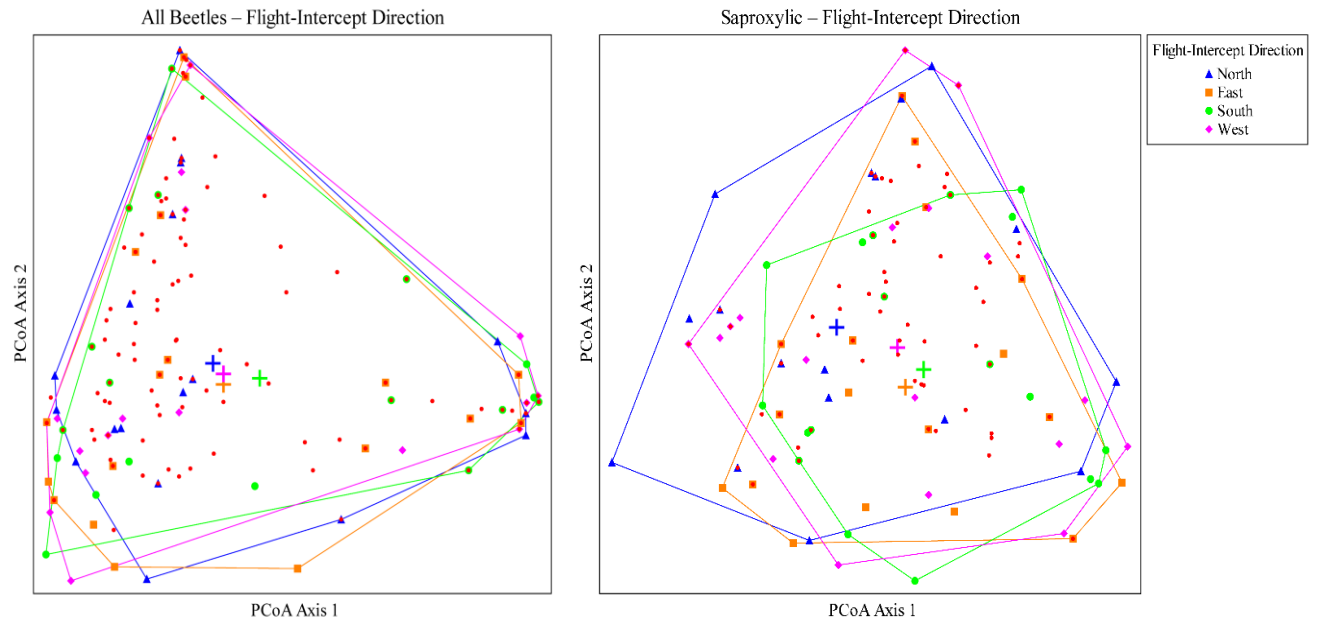


Fig. 6 Principal Coordinates Analysis (PCoA) ordination plots of beetle assemblages sampled across the four flight-intercept bottle directions: blue triangles represent north-facing bottle directions; orange squares represent east-facing bottle directions; green circles represent south-facing bottle directions; and purple diamonds represent west-facing bottle directions. Red dots represent the positioning of beetle species across ordination space. Coloured convex hulls (polygons) outline beetle species associated with each flight-intercept bottle direction, while coloured crosses indicate group centroids (multivariate means) for each direction category. Ordination plot on the left shows results for the “All Beetles” group, while the plot on the right shows results for the “Saproxylic” group

The MRPP tests found non-significant results for both groups (“All Beetles”: $p = 0.964$, $A = -0.010$; “Saproxylic”: $p = 0.632$, $A = -0.002$). Additional PCoA and MRPP analyses with samples grouped by FT indicated that sampling-location effects significantly influenced IT assemblage composition across both beetle groups, with stronger effects observed within the “All Beetles” group (“All Beetles”: $p < 0.001$, $A = 0.307$; “Saproxylic”: $p < 0.001$, $A = 0.172$). For both beetle groups, ISA tests found no significant indicator species and randomisation tests for the sum of IVmax were non-significant (“All Beetles”: $p = 0.749$; “Saproxylic”: $p = 0.545$).

3) Beetle Assemblage Correlations:

Mantel tests showed no significant correlations between IT and ET beetle assemblages for either beetle group. For both groups, a significant, positive correlation was found between IT and PT beetle assemblages (“All Beetles”: $r = 0.314337$, $p = 0.010$, “Saproxylic”: $r = 0.276719$, $p = 0.009$). Note also that there were no significant correlations between ET and PT assemblages.

Discussion

Across all trap types, sampling captured a diverse beetle assemblage, spanning a broad range of functional groups. Over half of the species, and a significant proportion of the specimens recorded, were saproxylic, reinforcing the value of multi-method sampling strategies for capturing this under-represented, high-priority group. Sampling also yielded species of conservation interest, including woody old-growth indicators, and three new Irish species, i.e., *Biblopectus pusillus* (Denny, 1825), *Corticaria longicornis* (Herbst, 1783) (unique to ITs respectively), and *Sericoderus brevicornis* Matthews, 1890 (recorded in ITs and PTs) (Crowe et al. in prep.) (Online Resource 1: Table S2 Full Species List). Importantly, analysing both the entire beetle assemblage and the saproxylic subset provided complementary insights into sampling performance. Specifically, while observed patterns were broadly consistent across both beetle groups, compositional differences were slightly stronger for the saproxylic subset, particularly in relation to Trap Type effects. These patterns are further explored below.

Trap Type Efficacy

Trap Type significantly affected the abundance and species richness of both beetle groups, with consistent patterns observed: ITs recorded the highest values, ETs yielded the lowest, with PTs intermediate. As each method sampled different woodland strata and microhabitats, these results were expected and, consistent with previous studies (Okland 1996; Ranius and Jansson 2002; Hyvärinen et al. 2006; Quinto et al. 2013; Skvarla and Dowling 2017; Peuhu et al. 2019; Egorov et al. 2024) demonstrate that trap types, even when deployed in close proximity, yield significantly different results due to variation in design, efficiency, and selectivity. Here, ITs contributed ~86% of the total specimens and ~72% of the total species found. Furthermore, they captured 28 of the 32 families found, including seven unique to the trap type (Online Resource 1: Table S3). This relatively strong performance aligns with previous studies and highlights their capacity to sample a substantial proportion of the beetle assemblage (Ranius and Jansson 2002; Hyvärinen et al. 2006; Alinvi et al. 2007; Bouget et al. 2008a; Sverdrup-Thygeson and Birkemoe 2009; Quinto et al. 2013; Parisi et al. 2019). This high effectiveness is likely driven by IT placement and function. They are accessible to beetles in flight from multiple directions and sample individuals moving across a broader spatial extent within the woodland. As they are not restricted to specific microhabitats or substrates, they capture a wider range of species than more targeted trap types. However, this also represents a key limitation of ITs, as they cannot provide direct evidence of substrate use by beetle species (Ranius and Jansson 2002; Wikars et al. 2005; Alinvi et al. 2007; Bouget et al. 2008a), limiting their ability to infer species-habitat associations or developmental substrates. Furthermore, despite their relatively high efficiency, ITs did not capture

the full assemblage here and missed 28% of species, added to the study by ETs and PTs. Thus, a substantial proportion of the beetle fauna would have been overlooked if ITs were used in isolation here. These findings support the central role of ITs in woodland beetle sampling, while also highlighting that, like all methods, ITs are inherently selective. Thus, combining ITs with complementary methods broadens the range of beetle taxa detected.

Emergence traps directly sampled saproxylic habitat and were important to record species underrepresented by the other trap types. Given their specialised function, it is unsurprising that they collected the highest *proportion* of saproxylic species, relative to the total species collected in each trap type (ETs: 63%; PTs: 57%; and ITs: 56%). They also captured 18 of the 32 families recorded overall, including three unique families (Online Resource 1: Table S3). Despite these strengths, ETs consistently recorded the lowest abundance and species richness across both beetle groups, with three traps yielding no beetles across the sampling period. Similar patterns have been reported in previous studies, indicating that ETs sample a more restricted subset of the beetle assemblage (Okland 1996; Wikars et al. 2005; Alinvi et al. 2007). These lower ET capture rates are largely driven by their inherent function, as their assemblage composition and overall effectiveness are strongly influenced by the restricted volume, diversity (e.g., small branches versus large logs) (Schiegg 2001; Macagno et al. 2015), and condition (e.g., decay class, tree species) (Kappes and Topp 2004; Lee et al. 2014) of woody substrates enclosed within the trap. This constraint can also introduce sampling bias and variability, effects that were mitigated here by randomly selecting woody substrates and standardising samples by weight and decay class. Beetle life history traits likely also influenced capture rates, as many saproxylic species have prolonged developmental periods (2-10 years) within wood (Martikainen and Kaila 2004; Buse et al. 2007; Alexander and Anderson 2012; Gallardo and Cárdenas 2016; Soutinho et al. 2025). Consequently, not all individuals present within a sampled substrate will emerge during the sampling period. Furthermore, as emergence traps are known to modify the natural conditions surrounding sampled dead/decaying wood, including airflow, moisture, and temperature, altered microclimatic conditions within the enclosed ET structures may have influenced emergence rates (Seibold et al. 2016; Lindman et al. 2022). While these effects were not directly quantified here, continued beetle emergence across two summer periods suggests that conditions within the traps remained suitable for beetle development. Nevertheless, subtle microclimatic shifts may still have influenced capture rates to some degree. The direct effects of such are poorly quantified in the literature, however, and the extent to which these shifts influence insect development, emergence rates, and the decomposition of dead/decaying wood inside ETs remains largely unknown (Okland 1996; Alinvi et al. 2007; Jonsell and Hansson 2007; Ferro and Carlton 2011).

Although deployed for a shorter period (within the same sampling season), PTs collected significantly greater beetle abundance and species richness than ETs. This trend was consistent for both beetle groups, and across GLMs both adjusted and unadjusted for sampling effort, indicating that differences were not artefacts of unequal sampling effort. Surprisingly, they also captured a comparable *proportion* of saproxylic species, relative to their total catch, as ITs. Furthermore, they captured 17 of the 32 beetle families found overall, and contributed one unique family (Online Resource 1: Table S3). These results demonstrate that, under the current study conditions, PTs were particularly effective for sampling woodland-associated and saproxylic beetles. This strong performance, combined with their relative ease of set-up and ability to target flower-visiting (pollinator) species, highlights their complementary value in multi-method sampling approaches, and supports their increased use in similar woodland studies. The relatively strong performance of PTs here, particularly in comparison to the ETs, likely reflects a combination of factors related to their function and placement. The coloured bowls may have provided strong visual cues that attracted certain beetles, while their positioning in open sunspots likely increased encounter rates by targeting areas of higher beetle activity. In addition, their accessibility to flying beetles from the surrounding woodland may have contributed to higher captures, and sampling during periods of increased beetle activity may have played a role. Despite these advantages, however, PTs remained selective in the assemblages they captured, being biased towards flying species, and those small in size (average body length: ETs = 5.03mm; ITs = 3.27mm; and PTs = 2.77mm). Furthermore, they likely attracted certain species, while underrepresenting others, and due to their sensitivity to weather conditions were deployed for short sampling periods, thereby capturing only a limited window of beetle activity (Baum and Wallen 2011; Vrdoljak and Samways 2012; Saunders and Luck 2013; Ernst et al. 2016; Wang et al. 2017; Westerberg et al. 2021; Egorov et al. 2024).

Similar to abundance and species richness, Trap Type also significantly influenced assemblage composition. Across both beetle groups, minimal species overlap was observed, and each trap type contributed unique species. The ITs captured the highest proportion of unique species and specimens for both beetle groups, highlighting their ability to sample a broad range of beetles, likely mobile taxa, using the woodland shrub layer. Emergence traps captured a lower proportion but provided a distinct assemblage, likely comprising less mobile (though many species are capable of active flight as adults) and more specialised species. Pan traps captured the lowest proportion of unique captures but also contributed a distinct subset of species, likely visually-oriented, flower-visiting taxa using the woodland field layer. These compositional differences were confirmed as statistically significant, with MRPP results indicating slightly stronger effects on the “Saproxylic” group. This pattern likely

reflects the direct sampling of dead/decaying wood within the ETs, which selectively targeted saproxylic species. However, this effect may have also been reinforced by the specialised ecologies of saproxylic species, including their narrow microhabitat associations and, in some cases, limited dispersal ability. Although the adults of many saproxylic species can utilise other resources (e.g., flowers), their life cycle remains closely linked to saproxylic (dead/decaying wood) microhabitats. These traits may increase their sensitivity to trap design and spatial positioning (Grove 2002; Bouget et al. 2008a; Quinto et al. 2013; Micó et al. 2020; Winiger et al. 2023). In contrast, the “All Beetles” group encompasses a broader range of taxa with diverse ecological functions, including species less tightly constrained by specific substrates or microhabitats. Therefore, these species may be less influenced by trap placement or design (see also supplementary exploratory analyses comparing “Saproxylic” and “Non-Saproxylic”, i.e., “All Beetles” subset excluding saproxylic species, assemblage responses to Trap Type, which identified comparatively weaker compositional structuring within the “Non-Saproxylic” group; Online Resource 1: Appendix A). PERMDISP tests further revealed significant differences in dispersion among trap types across both beetle groups (“All Beetles” and “Saproxylic”), indicating that differences were not driven solely by shifts in species composition, but also by differences in how consistent assemblages were across samples. This likely reflects variation in method selectivity and sensitivity to local environmental conditions, with some trap types capturing more heterogeneous, localised subsets of the assemblage, while others sampled a more consistent component of the beetle community. In addition, ISA analyses found statistically significant species associations with each trap type, particularly ITs (Online Resource 1: Table S4). Taken together, these findings demonstrate strong partitioning of assemblages among trap types across both beetle groups, and highlight the value of using a combination of sampling methods for woodland beetles.

Effect of Pan Trap Colour

Pan Trap Colour significantly affected beetle abundance for both beetle groups, with blue bowls capturing more specimens than white and yellow bowls. Given the proven effectiveness of white and yellow PTs in beetle studies (Campbell and Hanula 2007; Cavaletto et al. 2020, 2021), this result was unexpected. Nevertheless, many studies have reported beetle attraction to blue traps, including for saproxylic species (Campbell and Hanula 2007; Cavaletto et al. 2020, 2021; Vuts et al. 2022). While the factors driving these patterns remain unclear, blue bowls may have resembled blue-violet-flowering plants in the woodland which are preferred by some beetle species over white and yellow flowers. However, it is likely that these observed patterns reflect differences in visual perception and contrast, rather than simply colour mimicry. Blue bowls may have provided greater chromatic contrast against the woodland surroundings (Cavaletto et al. 2021; Caves et al. 2024; Dodds et al. 2024; Besana

et al. 2025), particularly given that blue is a relatively uncommon colour in nature. Thus, blue PTs may have appeared more visually conspicuous and attractive to some beetles. Species richness was not significantly affected by PT Colour. This finding is consistent with previous studies, although some mixed, species-specific responses have been reported (Rassati et al. 2019; Cavaletto et al. 2021). Therefore, while blue bowls captured a greater number of beetle individuals here, they did not sample a broader spectrum of species; instead, they likely captured a higher abundance of a smaller number of dominant taxa. This pattern indicates that reliance on a single bowl colour may bias sampling towards certain taxa, highlighting the importance of using a combination of colours to obtain a more representative species pool.

In contrast with species richness, significant differences in assemblage composition were observed among PT colours for both beetle groups. This finding is notable and demonstrates that, had analyses been based on species richness alone, important compositional patterns would have been overlooked. This highlights the value of evaluating multiple community metrics together in research studies to potentially provide more comprehensive ecological insight. Each PT colour (blue, white, yellow) captured unique species, relative to the entire PT catch. Blue bowls contributed the highest proportion of unique captures for both beetle groups, emphasising their relatively strong performance in capturing distinct taxa. Yellow bowls contributed more unique captures than white for the “All Beetles” group, whereas the opposite was true for the “Saproxyllic” group. The drivers underlying this contrasting pattern remain unclear. Across both beetle groups, relatively low species overlap suggests that colour responses are species-specific and suggests that the inclusion of multi-coloured traps may enhance the taxonomic breadth of a sampling strategy. Multivariate analyses further supported these patterns. Across both groups, PCoA plots showed partial overlap among PT colours, suggesting that although some species were shared, assemblages were not identical across colours. The results of MRPP analyses confirmed these differences as statistically significant, and subsequent PERMDISP tests were non-significant, indicating that these patterns were not driven by differences in assemblage dispersion, but instead reflect true compositional turnover among colours. Notably, these effects were slightly stronger for the “Saproxyllic” group. Although not directly tested here, this may reflect their specialised reliance on specific visual cues when locating suitable tree hosts or microhabitats (Cavaletto et al. 2020, 2021) (see also supplementary exploratory analyses comparing “Saproxyllic” and “Non-Saproxyllic” assemblage responses to PT Colour, which identified comparatively weaker compositional structuring within the “Non-Saproxyllic” group; Online Resource 1: Appendix A). Furthermore, ISA identified statistically significant species associations for each PT colour. Collectively, these findings suggest that different coloured PT bowls, even when placed in close proximity to one another, can sample distinct components of the

beetle assemblage, demonstrating the value of using a combination of trap colours to increase the taxonomic breadth of sampling.

Effect of Flight-Intercept Bottle Direction

Flight-Intercept Bottle Direction significantly affected the abundance of the “All Beetles” group only, with north-facing bottles capturing significantly fewer beetles than south and west-facing bottles. There were no significant effects observed, however, for the species richness of either beetle group. This suggests that directional effects may have been largely driven by a subset of numerically dominant, non-saproxyllic species from the “All Beetles” group, which were more frequently captured in south and west-facing bottles. This would, therefore, explain the non-significant results for the abundance of the “Saproxyllic” group, and for the species richness of both groups. Reduced capture rates in north-facing bottles were most likely an artefact of trap placement. Flight-intercept traps are passive (non-baited), activity-based traps, and differences in captures among directions, therefore, likely reflect increased beetle movement within these air-zones rather than true directional preference. Each IT was hung on the south side of an FT and positioned 30cm from the tree trunk. This trap placement, combined with the orientation of the four bottle openings in the cardinal directions, meant that north-facing bottles were always positioned closest to, and facing towards, the tree trunk. This close proximity to the tree trunk likely reduced the available flight space immediately in front of the north-facing bottles, physically obstructing beetle flight and limiting their ability to enter the trap. In contrast, the relatively stronger-performing south and west-facing bottles were unobstructed by the FT and more accessible to flying beetles. Notably, previous studies have shown that trunk-mounted ITs can yield distinct beetle assemblages compared to free-hanging designs, emphasising that trap placement relative to the tree the trap is hung on can strongly influence beetle captures (Sverdrup-Thygeson and Birkemoe 2009). Therefore, if ITs in the current study had been attached directly to, or positioned further from, the tree trunks, different patterns may have been observed. These findings highlight the importance of trap placement and design in shaping sampling outcomes in woodland beetle studies. While trap placement likely represents the primary driver of the observed patterns, other factors may have contributed. This includes Ireland’s prevailing south-westerly winds (Met Éireann n.d. b), which may have increased the likelihood of beetles being intercepted by south and west-facing bottles when flying downwind or passively carried by the airflow. Furthermore, species-specific flight behaviour (e.g., movement towards host trees for food, mating, or oviposition sites) (Byers 1999; Evenden et al. 2014; Jones et al. 2019; Wijerathna and Evenden 2020) may have influenced interception rates to some degree. These mechanisms remain unconfirmed, however, and require further research to disentangle their relative effects.

Similarly to species richness, no significant differences in assemblage composition across IT bottle direction were recorded for either beetle group. This suggests that directional effects do not strongly influence overall assemblage structure. Despite these findings, across both beetle groups, each IT direction contributed some unique species relative to the entire IT catch. East-facing bottles yielded the highest proportion of unique captures, followed by south, north, and west-facing bottles. These species would also have been captured in conventional ITs; however, the direction of their entry would have been overlooked, as beetles intercepted from all directions are typically funnelled into a single collector (Bouget et al. 2008a; Sverdrup-Thygeson and Birkemoe 2009; Sbaraglia et al. 2025). Thus, retaining separate samples for each IT direction may reveal subtle ecological patterns in species-specific behaviour, which could inform ecological understanding and future sampling approaches. Overall, our results indicate that directional effects were ecologically minor and did not reflect strong structuring of the beetle assemblage. Nevertheless, retaining directional data within ITs may reveal species-specific ecological insight.

Beetle Assemblage Correlations

Mantel tests found no significant correlations between IT and ET assemblages for either beetle group. This was unsurprising given that each trap type targeted different woodland strata and microhabitats, and as such, collected different ecological components of the overall beetle assemblage, i.e., ITs likely sampled flying adult beetles using the woodland shrub layer, while ETs likely sampled species emerging from grounded dead/decaying wood, many of which have substrate-associated larvae, but may also have adult stages capable of flight. This indicates that, within the current woodland system, using ITs alone would have overlooked additional taxa targeted by ETs, highlighting the complementary value of using these two trap types in tandem. In contrast, significant, positive correlations were found between IT and PT assemblages. Notably, this pattern holds true for the “Saproxyllic” beetle group, demonstrating that despite their uncommon use in saproxyllic beetle studies, PTs here were relatively effective and captured a similar assemblage to that of the widely used ITs. This overlap has potentially important practical implications: in studies with similar woodland conditions, where trap simplification is required (e.g., due to resource limitations), PTs could be omitted, provided that ITs are retained. However, while correlated, each trap type captured unique species, and removing any individual method would reduce the ecological breadth of the sampled assemblage. Therefore, trap selection should balance logistical feasibility with the overarching goal of capturing a broad range of beetle taxa, as further discussed below. Note also that no significant correlations were found between ETs and PTs for either beetle group, highlighting the value of including ETs in woodland beetle surveys, particularly when targeting saproxyllic species.

Practical Considerations and Future Recommendations

Ecological sampling strategies should be designed to: a) effectively capture the target taxa; and b) address the specific research questions posed. However, practical constraints including time, cost, logistical feasibility, health and safety, and habitat context are also critical considerations when selecting appropriate sampling methods (Alinvi et al. 2007; Cohnstaedt et al. 2012; Montgomery et al. 2021; Devi et al. 2025; Hoffmann and Stoll 2025). In the current study, traps were handmade to reduce costs and enable the deployment of higher trap numbers. However, trap construction added considerable time and effort; beyond construction, additional time and effort were required to deploy and dismantle traps, and collect, sort, and store resulting samples. For practical and ethical reasons, these factors should be carefully considered before sampling begins. Furthermore, given that all sampling methods have inherent strengths and weaknesses, it is essential to identify which aspects of trap efficacy are most critical for the objectives of a study before selecting methods accordingly (Table 8). This approach may help to clarify how different methods can be combined to complement one another and account for their inherent limitations, while also identifying redundant combinations due to similarities in design and function. Detailed efficiency rankings for the trap types used in the current study, along with additional methodological recommendations to improve sampling strategies are presented in Table S5 and S6 (Online Resource 1).

Table 8 Summary of the practical strengths, limitations, and recommended applications of each trap type: flight-intercept (IT), emergence (ET), and pan (PT) traps

Trap	Pros	Cons	Recommended Use
IT	Cost-effective and easy to construct	Time-intensive sample processing	Baseline inventories, long-term monitoring, and comparative studies. Should be combined with targeted methods to improve detection of specialised saproxylic taxa
	Moderate effort required to deploy and disassemble	Bias towards flying species.	
	Robust to environmental conditions	Captures non-saproxylic (“tourist”) species, and limited ability to confirm substrate association	
	Relatively easy to standardise		
	High sampling efficiency		
ET	Efficient sample collection and processing	Time-consuming to install/dismantle	Targeted saproxylic studies, particularly those determining microhabitat use, phenology, and larval developmental sites. Not sufficient alone for broad inventories or community-level comparisons
	Robust to environmental disturbances	Higher construction costs, and relatively difficult to standardise	
	Directly samples saproxylic habitat	Efficiency dependent on substrate selection	
	Can operate over extended periods	Lower trapping efficiency	
PT	Cost-effective, rapid deployment and collection	Highly sensitive to weather conditions	Short-term research studies, pollinator-focused studies, and investigations of visual ecology. Should be used alongside other methods to improve overall assemblage coverage
	Low sample processing time	Provide short sampling window	
	Effective for flower-visiting and visually orientated taxa	Require longer preparation time (due to paint-drying time)	
	Can detect colour preferences	Bias towards small, flying species	

Given that this study was limited to a single woodland system and conducted over one summer sampling period, future research aiming to replicate or expand upon this work should implement the sampling strategy across a broader range of woodland sites and types, geographic regions, and temporal scales. Furthermore, where feasible and ethically justified, sampling effort could be increased and complemented with active-sampling approaches, such as hand-searching. Such research would improve understanding of how woodland beetle assemblages and sampling-method performance vary across ecological contexts, while also enhancing the detection of rare, cryptic, and specialised taxa. In turn, findings from these studies would strengthen baseline biodiversity inventories and

further refine evidence-based sampling strategies for both general woodland and specialised saproxylic beetle research and conservation.

Conclusions

This study demonstrates that trap type and design can strongly influence woodland beetle assemblages, particularly saproxylic species, affecting abundance, species richness, and assemblage composition. Overall, our findings indicate that using a multi-method sampling approach can broaden the range of beetle taxa detected. More specific to our research questions, we found that:

1. Flight-intercept traps were highly effective as a core sampling method, capturing the majority of beetle species and individuals; however, no single method captured the full range of beetle taxa detected across all trap types. Emergence and PTs contributed distinct taxa and complementary components, together accounting for a substantial proportion of species that would have been overlooked if ITs were used in isolation. Combining these trap types within a single integrated sampling strategy, therefore, broadened the range of beetle taxa detected and increased taxonomic breadth.
2. At a finer scale, trap design also influenced sampling outcomes. Pan trap colour affected both beetle abundance and assemblage composition, with blue bowls capturing the highest abundance, and all colours sampling distinct assemblage components. Directional effects were observed for overall abundance, but were likely driven by trap placement rather than true ecological preference. While minimal, these patterns may provide fine-scale ecological information regarding species-specific flight behaviour. These results suggest that incorporating variation in trap design can further enhance sampling effectiveness.
3. Woodland studies comparable to this work, which require reduced sampling effort, may omit PTs to *minimise* ecological data loss provided ITs are retained, although some species will inevitably be missed.

Importantly, evaluating sampling performance across both the full beetle assemblage and the saproxylic subset provided valuable ecological insight, capturing both broader assemblage patterns and those specific to saproxylic species. Within the context of Ireland's poorly described saproxylic fauna, this study provides an important methodological foundation for improving faunistic baseline data. It offers an effective framework for generating

ecologically meaningful datasets, supporting biodiversity assessment, and conservation-focused research on woodland beetles, particularly saproxylic species.

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