

*A Diversity of Methods for a Diversity of Beetles: Complementary Approaches to Woodland
Sampling – A Case Study.*

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Abstract

Saproxylic beetles are declining across Europe due to habitat loss and limited ecological understanding. Effective, standardised sampling strategies are, therefore, required to monitor their populations and inform 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. Analyses were conducted on the entire beetle assemblages and their saproxylic subsets, thereby addressing a conservation-priority group, while also informing general beetle monitoring. We also tested pan trap colour and flight-intercept bottle direction effects on capture rates, and assessed trap-specific assemblage correlations to evaluate sampling method overlap and complementarity.

Trap type significantly affected capture rates. Flight-intercept traps collected the greatest abundance and species richness. However, all methods sampled distinct assemblage components and unique species. Pan trap colour significantly affected beetle abundance. Blue bowls outperformed white and yellow; however, all bowl colours captured unique assemblage subsets. Flight-intercept bottle direction influenced overall beetle abundance, with north-facing bottles capturing significantly fewer specimens than south and west-facing bottles. All bottle directions captured unique assemblage subsets. Flight-intercept and pan trap assemblages were significantly correlated.

We demonstrate that multi-method sampling strategies are required to capture representative woodland beetle assemblages, including for saproxylic species. Flight-intercept traps should form the core sampling method, supplemented with emergence and pan traps to broaden species coverage. Where resources are limited, pan traps may be omitted, provided flight-intercept traps are retained.

Implications for Insect Conservation

Our findings strengthen the standardisation and accuracy of woodland beetle monitoring, providing a robust evidence base for conservation planning. Understanding how trap type and design influence sampled beetle assemblages enables more representative biodiversity assessments and long-term population monitoring. These findings also inform the development of conservation tools such as habitat scorecards, national species lists, and European Red-List assessments.

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

Introduction

Saproxylic species are those involved in or dependant 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. 2008; Stokland and Meyke 2008) and provide important ecological services, including: deadwood decomposition, nutrient-cycling (Siitonen 2001; Stokland et al. 2012; Ulyshen 2016; Micó et al. 2020), and pollination (Gutowski 1990). They are also 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 has 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 and lack of ecological knowledge regarding species status and requirements (Nieto and Alexander 2010). Thus, further saproxylic beetle research and conservation is required.

Effective sampling and monitoring strategies are required to determine species status and inform conservation efforts. Saproxylic beetles, particularly those inhabiting woodlands, are difficult to sample (Kitching and Stork 2001; Martikainen and Kouki 2003; Martikainen and Kaila 2004; Bouget et al. 2008; Leather 2005; Stokland et al. 2012; Andersson et al. 2014; Ulyshen 2018; Burner et al. 2022; Brockerhoff et al. 2023; Crowley et al. 2023; Mendicino et al. 2025), and capturing a full, representative assemblage requires more than one sampling method. Thus, multi-method sampling approaches, each targeting different woodland microhabitats, are often used. 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, heretofore, no studies have simultaneously compared flight-intercept, emergence, and pan traps, or hand-made trap designs that are assessed in this study. Moreover, few European studies have compared compositional patterns across both the entire beetle assemblages, and their saproxylic subsets. Saproxylic species may respond differently to general sampling methods (Grove 2002; Bouget et al. 2008; Quinto et al. 2013; Micó et al. 2020; Winiger et al. 2023). Thus, evaluating trap performance for them specifically is vital to ensure accurate monitoring of saproxylic beetle populations. Within this wider European context, Ireland provides an especially relevant case study, where monitoring and conservation of saproxylic beetles remains 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 be subject to distinct isolation, climate, and habitat pressures, as has been demonstrated for other woodland insects of conservation interest, e.g., the Hairy Wood Ant: *Formica lugubris* Zetterstedt, 1838 (Formicidae) (Mäki-Petäys and Breen 2007). While not yet studied, Irish saproxylic beetle fauna may differ ecologically and behaviourally to their British and European counterparts, as research suggests that range-edge insect populations can display altered dispersal, phenology or life-history traits (Burton et al. 2010; Clark et al. 2022; Ittonen et al. 2022; Dederichs et al. 2024). This distinctive 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%), of which only 2% is composed of native species. Important old-growth habitats are scarce, fragmented and threatened. Notably, 50% of Irish saproxylic beetle species are considered rare, likely reflecting 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; Department of Agriculture, Food and the Marine 2023). 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 is already isolated from British and European sources, and within the island, populations are further separated by the extreme patchiness of native woodland (Perrin and Daly 2010; Alexander and Anderson 2012), creating a double pressure that increases vulnerability. More broadly, the Irish fauna provides 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. To realise this potential, effective monitoring strategies are essential, with

comparative methodological studies a necessary first step to reveal the selectivity, efficiency, and complementarity of different sampling methods.

We present the first study to simultaneously compare flight-intercept, emergence, and pan traps, for sampling woodland beetles. We assessed trap performance in capturing representative inventories of both the entire beetle assemblage, and the saproxylic subset, thereby addressing a group of conservation concern, whilst also ensuring broader relevance to general beetle research.

Our specific research aims were:

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 provide a representative characterisation of beetle assemblages, when compared with emergence and pan traps.

Findings will contribute to the development of standardised sampling of saproxylic beetles across Europe and guide evidence-based, Irish beetle monitoring.

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 and Prétesseille 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 2.72mm and average minimum and maximum temperatures are 6°C and 13°C respectively (Met Eireann n.d.). 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).

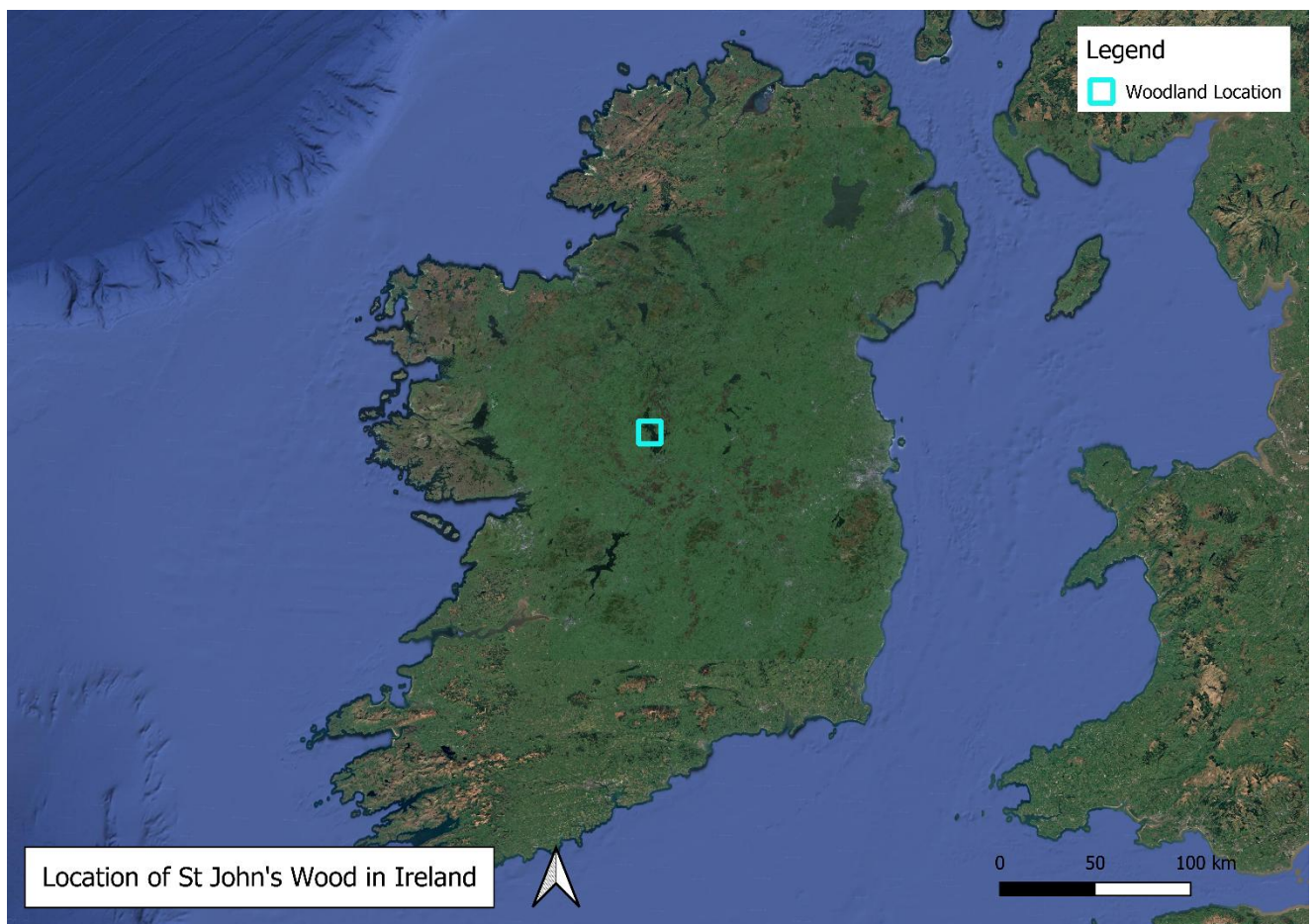


Fig. 1 Location of St John's Wood in Co. Roscommon, along Lough Ree, within the Irish midlands (Lat: 53.5523, Long: -8.0040). A Crowe 2025, QGIS

Sampling Strategy

Eighteen veteran *Q. robur* trees were randomly selected as focal trees (FTs) across the woodland (Fig. 2). All FTs were categorised as “veteran” using a specifically designed scorecard (Online Resource 1: Table S1) and were >50m apart to ensure trap independence and avoid spatial autocorrelation (Buse et al. 2008; Parmain et al. 2013; Allison et al. 2014; Burner et al. 2022). At each FT, three methods (Fig. 3) were used to trap beetles, each targeting different woodland strata: 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 branch of each FT, 1.5m above ground and 30cm from the tree trunk; 2) A pan trap (PT) (Campbell and Hanula 2007; Vrdoljak and Samways 2012; Crowley et al. 2023), placed in a pocket of light 10m east of each FT, collected beetles using the field layer; 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.

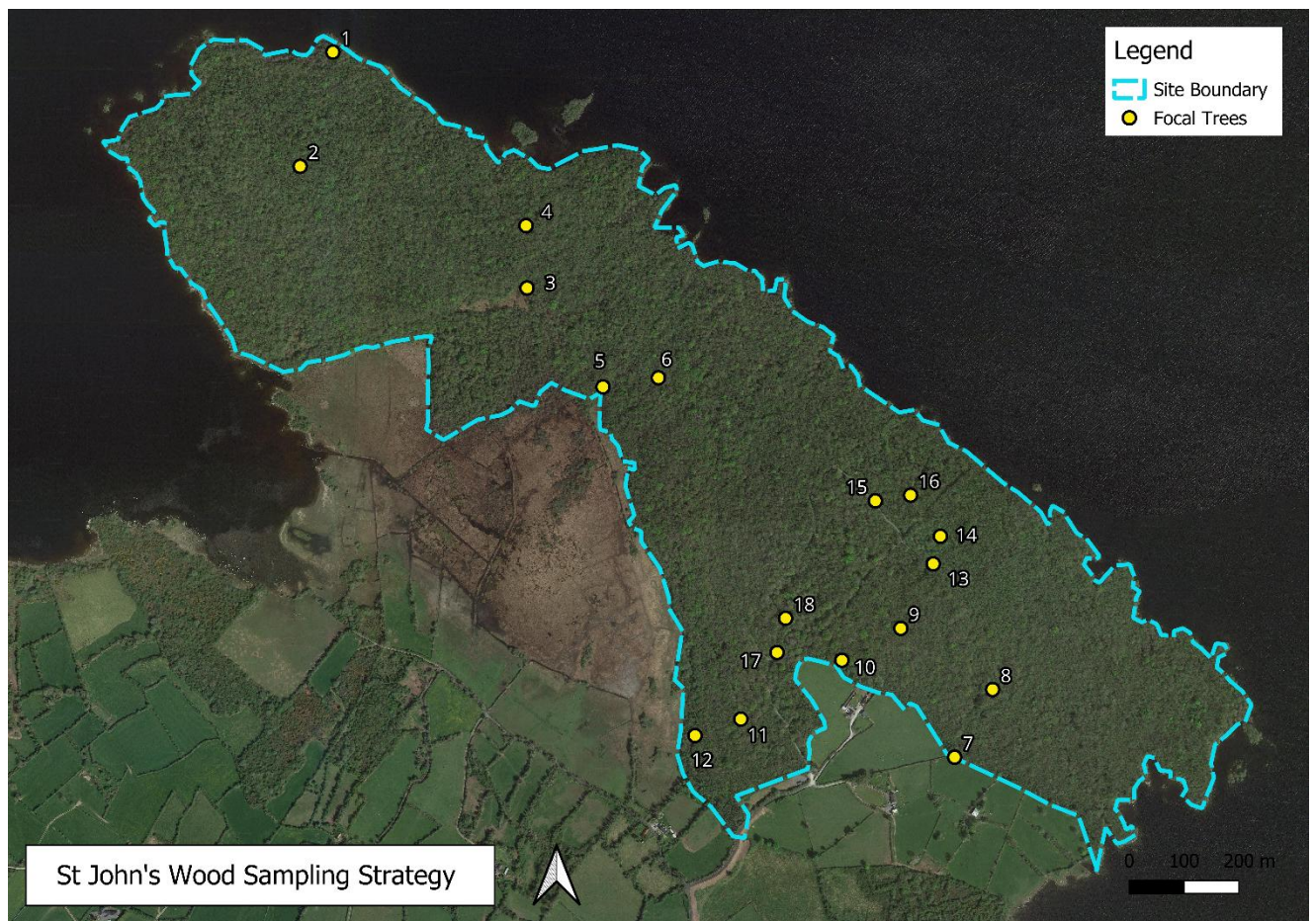


Fig. 2 St John's Wood sampling strategy showing the woodland site boundary in a blue hatched line, and the 18 randomly selected sampling locations (focal trees- veteran *Quercus robur* L. (Fagaceae)) in yellow dots. A Crowe 2025, QGIS



Fig. 3 Trap set-up at each focal tree (sampling location). One flight-intercept trap was hung on a south-facing tree branch of each focal tree, 1.5m high and 30cm from the tree trunk. Note each flight-intercept trap consisted of four upturned bottles, with surface openings facing in each of the cardinal directions. A pan trap was left ten metres to the east of each focal tree in a pocket of light. Note each pan trap consisted of three coloured bowls (blue, white and yellow). An emergence trap was left just north of each focal tree, in the shade. Each trapping method targeted different woodland stratum, i.e., ground layer, field layer and shrub layer (A Crowe 2022)

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 sampling 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 was based on, and modified from, Irmeler 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

Biweekly 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 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 to 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 beetle species combined, including known saproxylic species); and 2) “Saproxylic” (only known saproxylic species included). Analyses were carried out on both groups separately, with patterns across all Coleoptera being analysed before looking specifically at the saproxylic subset group. For the purposes

of this paper, beetle species which adhered to the following criteria were classified as saproxylic (Crowe et al. in prep.):

- Feed directly on dead/decaying wood or products of wood decay e.g. wood fungi/mould
- Have immature stages (includes larvae) that develop in: dead/decaying wood (includes woody plant stems e.g. dead/decaying Ivy); or in the products of wood decay e.g. wood fungi.
- Use the following saproxylic microhabitats - tree cavities, rot-holes, wood mould, nests in tree canopy/cavities.
- Are associated with tree sap.

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). 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. Note also, when testing for Trap Type effects, analyses were performed using both raw data and data adjusted for sampling effort. 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. Indicator Species Analysis (ISA) identified species that had statistically significant associations with specific groups. 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 - reduces 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* (Marsham, 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) “Saproxylic” consisting of only a subset of the species found, which were saproxylic in nature. Saproxylic beetles formed a substantial component of the overall beetle assemblage, accounting for 55% of the total species and 43% of all specimens found. Furthermore, saproxylic species were present in 22 of the 32 families recorded. These findings highlight their broad taxonomic representation and ecological significance within St. John’s Wood.

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”: $p = 0.005$; “Saproxylic”: $p = 0.011$), while ETs had significantly lower species richness than PTs ($p < 0.001$ for both beetle groups) (Online Resource 2).

Beetle Assemblage Composition

Venn diagrams show that across both beetle groups, each trap type captured unique species (Online Resource 1: Figs S4-S5). 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 2).

Table 2 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 beetles 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 NMS tests (Sørensen [Bray-Curtis] distance measure, maximum of six axes, 500 iterations, autopilot mode) found an optimal one-dimensional solution for both groups. Final stress values indicated solution stability (“All Beetles” = 0.00034, 44 iterations; “Saproxylic” = 0.02663, 137 iterations). A Monte Carlo test (250 randomized runs) confirmed the significance of these solutions (Axis 1 – “All Beetles” $p = 0.0040$; “Saproxylic” $p = 0.0080$). Due to the one-dimensional nature of these results, ordination plots were not included here. The PCoA tests (unimodal response data, Sørensen [Bray-Curtis] distance measure) found that the first three axes of the “All Beetles” group explained a substantial 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 clear separation between beetle assemblages across trap types, with minimal overlap between convex hulls. The first two axes of the “Saproxylic” group explained a substantial 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 that each trap type formed distinct assemblages, with no overlap between convex hulls.

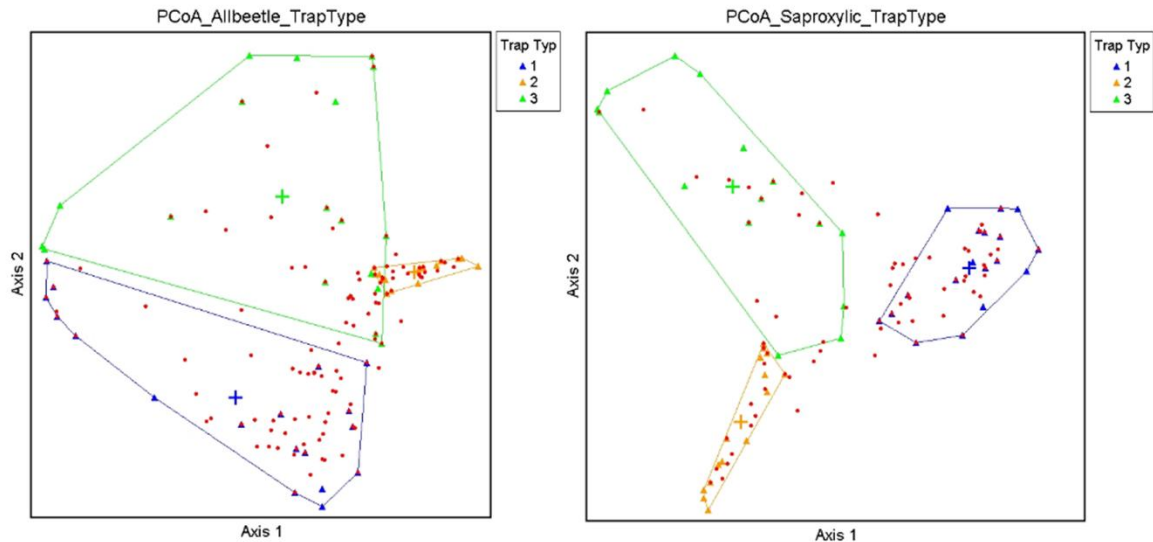


Fig. 4 Principle Coordinates Analysis ordination plots of beetle assemblage composition sampled across each of the three trap types: 1) Blue triangles represent flight-intercept traps; 2) Orange triangles represent emergence traps; and 3) Green triangles represent pan traps. Red dots represent the positioning 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” $p < 0.001$, $A = 0.120$). 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 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, with the exception of *Grynobius planus* (Fabricius, 1787) (Ptinidae) which was non-significant in the “All Beetles” dataset ($p = 0.052$). As indicator values for significant species varied between the two groups, results for both are provided (Table 3).

Table 3 Species Indicator Analysis results showing species with statistically significant associations with each of the three 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	0.007	27.8	Moderate	0.009*
<i>Agaricochara latissima</i> (Stephens, 1832)	PT	60.5	Strong	0.000	64.1*	Strong	0.000
<i>Anaspis rufilabris</i> (Gyllenhal, 1827)	IT	39.6	Moderate	0.002	44.2*	Strong*	0.002*
<i>Aleochara sparsa</i> Heer, 1839	IT	38.9	Moderate	0.001	38.9	Moderate	0.001*
<i>Biblopectus pusillus</i> (Denny, 1825)	IT	22.2	Moderate	0.032	N/A	N/A	N/A
<i>Baeocrara variolosa</i> (Mulsant & Rey, 1861)	IT	22.2	Moderate	0.027	22.2	Moderate	0.027*
<i>Cychramus luteus</i> (Fabricius, 1787)	IT	38.9	Moderate	0.001	38.9	Moderate	0.001
<i>Cartodere nodifer</i> (Westwood, 1839)	IT	41.5	Strong	0.016	N/A	N/A	N/A
<i>Cyphon padi</i> (Linnaeus, 1758)	IT	38.9	Moderate	0.001	N/A	N/A	N/A
<i>Cryptophagus saginatus</i> Sturm, 1845	IT	73.6	Very Strong	0.000	68.9*	Strong*	0.000
<i>Cryptophagus scanicus</i> (Linnaeus, 1758)	IT	88.9	Very Strong	0.000	88.9	Very Strong	0.000
<i>Dinaraea aequata</i> (Erichson, 1837)	ET	40	Strong	0.001	40	Moderate*	0.000*
<i>Exomias araneiformis</i> (Schränk, 1781)	ET	19.1	Weak	0.046	N/A	N/A	N/A
<i>Epuraea biguttata</i> (Thunberg, 1784)	IT	24.8	Moderate	0.032	26.1*	Moderate	0.031*
<i>Eusphalerum luteum</i> (Marshall, 1802)	IT	38.6	Moderate	0.013	N/A	N/A	N/A
<i>Epuraea pallescens</i> (Stephens, 1835)	PT	25.7	Moderate	0.020	26.5*	Moderate	0.019*
<i>Grynobius planus</i> (Fabricius, 1787)	IT	25.2	Moderate	0.052	28.5	Moderate	0.024
<i>Grammoptera ruficornis</i> (Fabricius, 1781)	IT	22.5	Moderate	0.028	24.4*	Moderate	0.026*
<i>Haploglossa villosula</i> (Stephens, 1832)	IT	61.1	Strong	0.000	N/A	N/A	N/A
<i>Ocys harpaloides</i> (Audinet-Serville, 1821)	ET	25.8	Moderate	0.015	25.6*	Moderate	0.010*
<i>Pogonocherus hispidulus</i> (Piller & Mitterpacher, 1783)	ET	26.4	Moderate	0.010	26.3*	Moderate	0.010*
<i>Stenichnus bicolor</i> (Denny, 1825)	IT	41.5	Strong	0.003	43.1*	Strong	0.002*
<i>Sericoderus brevicornis</i> Matthews, 1890	IT	37.6	Moderate	0.004	40.5*	Strong*	0.003*
<i>Sepedophilus nigripennis</i> (Stephens, 1832)	ET	20	Weak	0.025	N/A	N/A	N/A
<i>Salpingus planirostris</i> (Fabricius, 1787)	IT	28.7	Moderate	0.013	25.4*	Moderate	0.038*
<i>Salpingus ruficollis</i> (Linnaeus, 1761)	IT	33.3	Moderate	0.002	33.3	Moderate	0.002*
<i>Sciodrepoides watsoni</i> (Spence, 1813)	IT	77.8	Very Strong	0.000	77.8	Very Strong	0.000

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

Across both groups, all PT colours had unique species (Online Resource 1: Figs S6-S7), with blue bowls contributing the highest proportion of unique captures. Yellow bowls contributed more unique captures than white for the “All Beetles” group, while white bowls contributed more for the “Saproxylic group” (Table 4).

Table 4 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 optimal NMS solution for both groups was one-dimensional. Final stress values indicated stable solutions (“All Beetles” = 0.00882, 46 iterations; “Saproxylic” = 0.17641, 315 iterations). A Monte Carlo test (250 runs) confirmed the significance of the “All Beetles” group solution (Axis 1 $p = 0.0040$). A Monte Carlo test was not conducted for the “Saproxylic” group as the dataset was zero-inflated. The PCoA results showed that the first three axes of the “All Beetles” group explained a substantial 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 robust and valid.

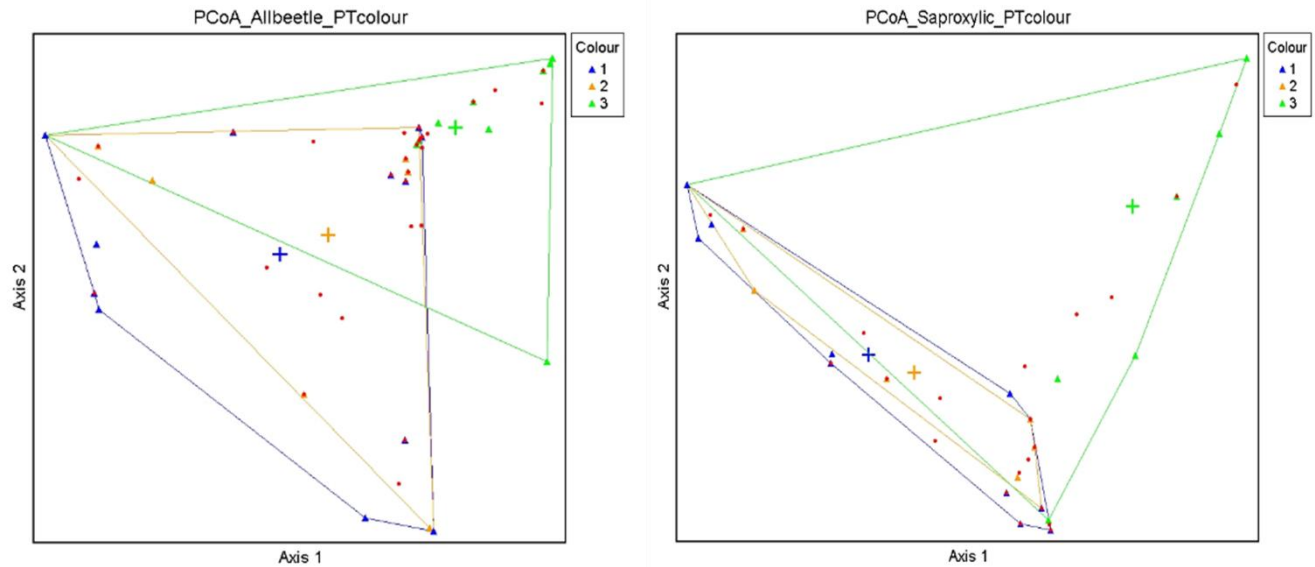


Fig. 5 Principle Coordinates Analysis ordination plots of beetle assemblage composition sampled across each of the three pan trap colours: 1) Blue triangles represent blue pan trap bowls; 2) Orange triangles represent white pan trap bowls; and 3) Green triangles represent yellow pan trap bowls. Red dots 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” $p < 0.001$, $A = 0.092$). The ISA results revealed species strongly associated with each colour (Table 5).

Table 5 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>Bibloporus bicolor</i> (Denny, 1825)	Blue	23.5	Weak	0.041	N/A	N/A	N/A
<i>Gyrophana minima</i> (Erichson, 1837)	White	18.7	Weak	0.094	27.9*	Moderate*	0.037*
<i>Cartodere nodifer</i> (Westwood, 1839)	Yellow	57.1	Strong	0.000	66.7*	Strong	0.000

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 groups, all IT directions had unique species (Online Resource 1: Figs S8-S9), with east bottles contributing the highest proportion of unique captures. South and north bottles captured a moderate share of unique captures, while west bottles contributed the lowest (Table 6).

Table 6 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	"Saproxylic" Unique Species	"Saproxylic" 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 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 NMS test found an optimal three-dimensional solution for the “All Beetles” group (final stress = 13.25782, 85 iterations). A Monte Carlo test (250 runs) confirmed the significance of the solution (Axis 3 $p = 0.0279$). The ordination plot (Fig. 6) shows considerable overlap in species among IT directions. A stable NMS solution was not found for the “Saproxylic” group, despite finding decreasing stress values with additional dimensions. The Monte Carlo test found a non-significant result ($p = 0.2032$).

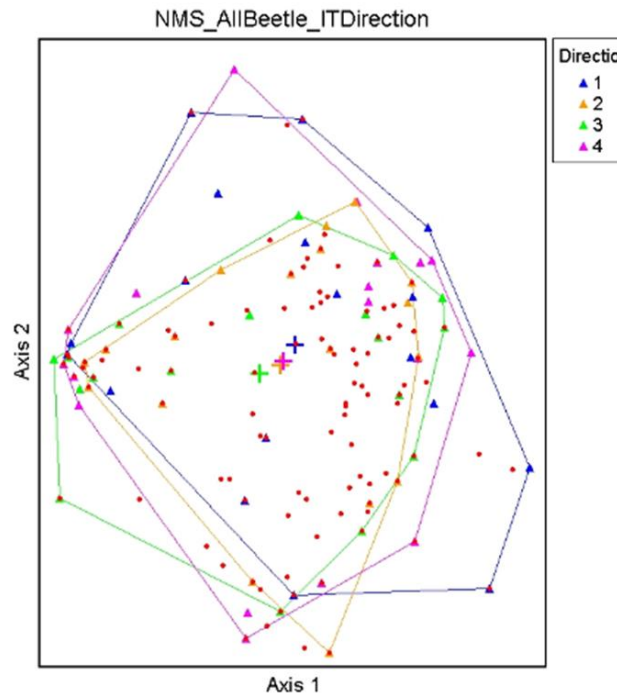


Fig. 6 Non-metric Multidimensional Scaling Ordination plot showing differences in beetle assemblages for the “All Beetles” group, across flight-intercept bottle directions: 1) Blue triangles represent north-facing bottle directions; 2) Orange triangles represent east-facing bottle directions; 3) Green triangles represent south-facing bottle directions; and 4) Purple triangles represent west-facing bottle directions. Red dots represent the positioning of beetles 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

The PCoA results showed that the first three axes of the “All Beetles” group explained a substantial 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. 7) 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 “Saproxylic”

group (Corrected cumulative % variance: Axis 1 = 9.246, Axis 2 = 17.551). The plot (Fig. 7) shows some separation between IT directions, however, there is substantial overlap.

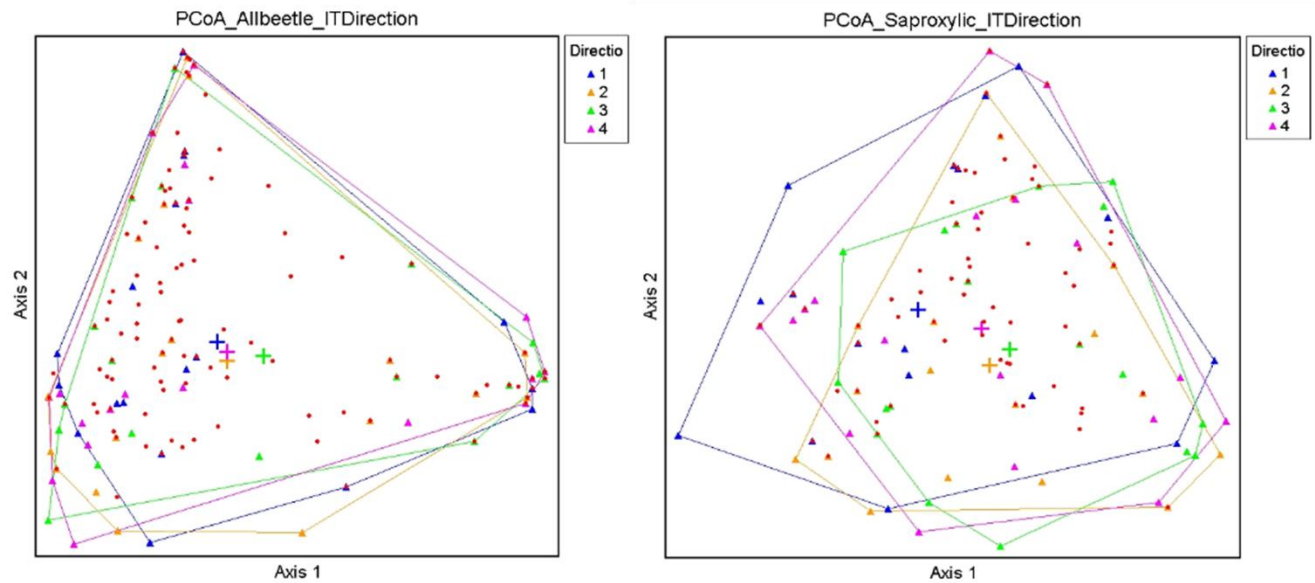


Fig. 7 Principle Coordinates Analysis Ordination of beetle assemblages sampled across the four flight-intercept bottle directions: 1) Blue triangles represent north-facing bottle directions; 2) Orange triangles represent east-facing bottle directions; 3) Green triangles represent south-facing bottle directions; and 4) Purple triangles represent west-facing bottle directions. Red dots represent the positioning of beetles 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” $p = 0.632$, $A = -0.002$). The ISA results are provided in Table 7.

Table 7 Species Indicator Analysis results showing species with statistically significant associations with flight-intercept (IT) bottle directions: north; east; south; and west. "All Beetles" group values are noted in the superscript ab columns, while "Saproxylic" values are noted in the superscript s columns

Species	IT Bottle Direction	Indicator ^{ab} Value	Indication ^{ab} Level	<i>p</i> Value ^{ab}	Indicator ^s Value	Indication ^s Level	<i>p</i> Value ^s
<i>Grammoptera ruficornis</i> (Fabricius, 1781)	East	14.9	Weak	0.064	16	Weak	0.039*
<i>Sericoderus brevicornis</i> Matthews, 1890	North	22.4	Moderate	0.045	23.5	Moderate	0.023*

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

3) Beetle Assemblages 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

Sampling captured a diverse beetle assemblage, spanning a broad range of functional groups, highlighting the range of critical ecological roles beetles play in woodland functioning. Over half of the species, and a significant proportion of the specimens recorded, were saproxylic, underscoring the ecological importance of these beetles within the woodland. 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), and *Sericoderus brevicornis* Matthews, 1890 (Crowe et al. in prep.). These findings reinforce the value of systematic sampling in under-surveyed habitats, particularly for under-represented insect groups.

This is the first Irish study to compare trapping methods for saproxylic and woodland-associated (non-saproxylic species, found within the woodland) beetles. Furthermore, no European studies have simultaneously compared ITs, ETs, and PTs for this faunal assemblage. While many studies have compared ITs and ETs (Okland 1996; Wikars et al. 2005; Alinvi et al. 2007; Quinto et al. 2013), none have used the specific trap designs deployed here, i.e., Carrel bottle IT and container ET, though similar designs have been used in isolation (Carrel 2002;

Wiesenborn 2009; Ferro and Carlton 2011; Alexander et al. 2014; Lee et al. 2014; Macagno et al. 2015; Hardersen et al. 2020). Thus, our sampling strategy is novel both nationally and internationally. We evaluated the influence of trap type, colour, and direction on beetle abundance, species richness, and composition, to guide future field sampling strategies and aid in methodological standardisation. These variable effects were evaluated across the entire beetle assemblage and separately on the saproxylic subset only, to capture broad ecological patterns, whilst also focusing on a key insect group of conservation concern. Saproxylic beetles are difficult to sample due to their taxonomic diversity, specialised ecologies, cryptic nature, and often limited dispersal (Martikainen and Kouki 2003; Martikainen and Kaila 2004; Bouget et al. 2008; Stokland et al. 2012; Andersson et al. 2014; Ulyshen 2018; Burner et al. 2022; Mendicino et al. 2025). These challenges are amplified when sampling in structurally complex woodlands (Kitching and Stork 2001; Leather 2005; Brockerhoff et al. 2023; Crowley et al. 2023), where traditional sampling methods may be less effective. As saproxylic species may respond differently to general trapping techniques used for other beetle groups, a core study aim here was to determine the most effective sampling methods for these species, despite inherent challenges. Testing effects across both beetle groups also ensured that sampling was robust and informed both general beetle biodiversity assessments and targeted saproxylic monitoring, which is vital for woodland management and conservation planning. Therefore, our results have broad-reaching relevance for anyone sampling woodland beetles, e.g., researchers, forest managers, and conservation practitioners.

Trap Type Efficacy

Trap Type significantly affected the abundance and species richness of both beetle groups (“All Beetles” and “Saproxylic”). This was expected, as each trap type targeted beetles using different woodland strata and microhabitats. In line 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), our results demonstrate that different trap types, even when set up near one another, yield significantly different results due to differences in design, efficiency, and selectivity. Across both beetle groups, ITs collected significantly greater abundance and species richness than ETs and PTs, while ETs collected the lowest values. These results were not surprising given IT placement and function. Flight-intercept traps capture beetles during flight. They are hung on south-facing tree branches, where beetle activity is likely higher, and sample beetles using the entire surrounding woodland area and adjacent habitats. Thus, ITs are known to collect high beetle abundance and species richness and are useful for community studies and site evaluations (Ranius and Jansson 2002; Hyvärinen et al. 2006; Alinvi et al. 2007; Bouget et al. 2008; Sverdrup-Thygeson and Birkemoe, 2009; Quinto et al. 2013). Here, ITs collected ~86% of the

total specimens, and ~72% of the total species found. In addition, they collected 28 of the 32 families found, with seven unique to the trap type (Online Resource 1: Table S2). However, ITs have limitations. They are biased towards collecting flying beetles and cannot prove that captured species were directly using the tree, on which the trap was hung (Ranius and Jansson 2002; Wikars et al. 2005; Alinvi et al. 2007; Bouget et al. 2008). Therefore, studies determining beetle microhabitat preferences, breeding or larval developmental sites, should supplement ITs with targeted trap types, such as ETs.

Emergence traps capture beetles emerging from enclosed woody-substrates. They provide direct evidence of local development and recruitment for a species, and can sample over extended periods. Thus, they are often used in saproxylic beetle studies (Schiegg 2001; Kappes and Topp 2004; Wikars et al. 2005; Alinvi et al. 2007). However, ETs are limited to sampling only those beetles using the small volume and diversity of dead/decaying wood enclosed in the trap. Furthermore, saproxylic beetles have markedly long and variable phenologies. Species can develop inside deadwood for 2-10 years before emerging (Martikainen and Kaila 2004; Buse and Assmann 2007; Alexander and Anderson 2012; Gallardo and Cárdenas 2016; Soutinho et al. 2025). Therefore, not all beetles inside the wood may emerge during the sampling period. These limitations likely contributed to the lower ET capture rates here, with three traps yielding no beetles at all. Lower capture rates are also noted in other studies. Thus, using ETs alone is not sufficient for large-scale site evaluations or community analyses (Okland 1996; Wikars et al. 2005; Alinvi et al. 2007). Irrespective of these drawbacks, ETs remained an important component of our study to target species underrepresented by the other trap types. Notably, 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 and contributed three unique families (Online Resource 1: Table S2).

However, despite being 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. These findings suggest that, under the current study conditions, PTs were particularly effective for sampling woodland-associated and saproxylic beetles, especially in comparison with the ETs. Pan traps visually attract and capture beetles by mimicking flowers. Their relatively strong performance here likely reflects a combination of factors: the coloured bowls emitted strong visual cues, attracting certain beetles; they sampled beetles using both the lower canopy and woodland field layers; their set-up may have coincided with peak flight periods; and they were placed in open sunspots, where beetle activity was likely higher. In

contrast, ETs depended on the slow and highly variable process of beetle emergence from dead/decaying wood. However, PTs are biased towards collecting flying beetles, and those small in size, a fact held true here (average body length: ETs = 5.03mm; ITs = 3.27mm; and PTs = 2.77mm). They attract certain species, while underrepresenting others, and are highly influenced by their surroundings, e.g., vegetation structure, floral presence, and are prone to damage from adverse weather, e.g., flooding or high winds (prevalent Irish conditions) (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). Therefore, they can only be set up for short periods and reflect only short beetle activity windows. Despite this, PTs added ecological value to the study. They captured 17 of the 32 beetle families found and contributed one unique family (Online Resource 1: Table S2). They collected significantly greater abundance and species richness of saproxylic beetles than ETs, and captured a comparable *proportion* of saproxylic species, relative to their total catch, as ITs. While PTs are rarely used in woodland beetle studies, our results support their increased use in future studies.

Trap Type also significantly influenced assemblage composition for both beetle groups. Minimal species overlap was noted, and each trap type contributed unique species. Across both beetle groups, ITs captured the highest proportion of unique species and specimens, 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 and more specialised species. Pan traps captured the lowest proportion of unique captures but also contributed a distinct subset of species, likely visually-oriented taxa using the woodland field layer. These compositional differences were confirmed as statistically significant, with results indicating slightly stronger effects on the “Saproxylic” group. This may be due to their more specialised ecologies, e.g., narrow microhabitat associations and limited dispersal ability, making them more sensitive to trap design and spatial positioning (Grove 2002; Bouget et al. 2008; Quinto et al. 2013; Micó et al. 2020; Winiger et al. 2023). In contrast, the broader “All Beetles” group likely includes more mobile, generalist species, which are less influenced by trap placement or design. In any case, the strong partitioning of assemblages across both groups underscores the importance of using a combination of trap types for these beetles. This is further supported by ISA results, which found statistically significant species associations with each trap type, particularly ITs (Online Resource 1: Table S3).

Effect of Trap Colour and Direction

Understanding how beetles perceive colour is key to interpreting their response to traps and provides insight into their ecological requirements. This information can inform effective sampling and conservation efforts (Cavaletto et al. 2021; Sukovata et al. 2022; Dodds et al. 2024; Miller 2025). Colour is a complex visual cue encompassing multiple dimensions, such as wavelength, reflectance pattern, intensity and contrast (Cavaletto et al. 2020, 2021; Sukovata et al. 2022; Dodds et al. 2024). Beetles are sensitive to these aspects and their responses are influenced by several factors, e.g., species, life-stage, sex, behaviour, and habitat context (Cavaletto et al. 2020; Sukovata et al. 2022; Vuts et al. 2022; Kuhn et al. 2024). Here, three PT colours (blue, white, and yellow), proven to be effective for sampling beetles (Campbell and Hanula 2007; Rubene et al. 2017; Cavaletto et al. 2021), were tested. Colour significantly affected beetle abundance for both beetle groups, with blue bowls capturing more specimens than both white and yellow bowls. This was unexpected, particularly for the “All Beetles” group, as research often reports the efficiency of yellow and white bowls, due to their resemblance to common flowering plants (Campbell and Hanula 2007; Cavaletto et al. 2020, 2021). Given that many yellow and white flowers were present in St. John’s Wood, we hypothesised that these colours would perform best. However, the woodland also supports blue-violet flowering plants. Blue bowls may have reflected similar wavelengths or intensity patterns as these flowers, thereby attracting certain beetles. Furthermore, although white and yellow bowls look brighter to the human eye, blue bowls may have provided greater chromatic contrast against the woodland surroundings for the beetles (Cavaletto et al. 2021; Caves et al. 2024; Dodds et al. 2024; Besana et al. 2025). Blue is a relatively uncommon colour in nature. Therefore, blue objects may appear more visually conspicuous and attractive to some beetles. While these explanations are not scientifically proven and require further research, they offer plausible ecological interpretations for the observed preference. Other studies have also reported beetle attraction to blue traps, including saproxylic species (Campbell and Hanula 2007; Cavaletto et al. 2020, 2021; Vuts et al. 2020). This is interesting given that beetles historically lost sensitivity to blue wavelengths, with some species regaining it through UV opsin duplication (Sukovata et al. 2022). Species richness was not significantly affected by PT Colour, aligning with findings in the literature, though some mixed species-specific responses have been noted (Rassati et al. 2019; Cavaletto et al. 2021). Therefore, while blue bowls captured a greater beetle abundance, they did not sample a broader spectrum of species. Instead, they likely sampled a larger number of a few dominant species, highlighting the importance of using a combination of bowl colours to collect a more representative species pool. Although few studies have tested PT Colour effects on beetles, many have tested coloured cross vane and funnel traps in invasive species monitoring. While black is the conventional choice, studies show that incorporating

additional colours broadens the captured species pool. Trap shape (long and horizontal) and colour (dark) are noted to attract saproxylic beetles by mimicking a tree silhouette (host), contrasting against a lighter background (McIntosh and Downey 2001; Bouget et al. 2008; Chen et al. 2010; Cavaletto et al. 2020; Miller 2025). Interestingly, a study using Artificial Neural Networks (ANNs) found that jewel beetles discriminate between leaves and bark (oviposition site) using visual signals from different photoreceptors. Purple PT bowls (similar wavelength as blue) were classified as bark, suggesting that the bowls might visually mimic oviposition sites (Sweeney et al. 2025). Another study indicated that broadleaf specialists may prefer grey or blue traps, based on host tree preferences (Cavaletto et al. 2020). These findings may explain why blue bowls here collected a higher number of saproxylic beetles, although further research is required to elucidate this relationship.

Regarding assemblage composition, all PT colours 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 at capturing distinct taxa. Yellow bowls contributed more unique captures than white for the “All Beetles” group, while the opposite was true for the “Saproxylic” group. These results indicate a possible relationship between trap colour effectiveness and the beetle functional group targeted. However, further research is required to elucidate this fully. Across both beetle groups, minimal species overlap was observed. This suggests that colour response is species-specific and highlights the importance of using a combination of trap colours to enhance the taxonomic breadth of a sampling strategy. Multivariate analyses also confirmed statistically significant differences in assemblage composition across PT colours for both beetle groups, though these effects were moderate in strength, relative to the influence of Trap Type. Notably, effects were slightly stronger for the “Saproxylic” group, possibly reflecting their specialised reliance on specific visual cues for locating suitable tree hosts or microhabitats (Bouget et al. 2008; Cavaletto et al. 2020, 2021). Further investigation is required to support this hypothesis fully, however. Across both groups, PCoA plots indicate similar overall patterns. Yellow bowls show the greatest species spread, suggesting that they captured a more compositionally diverse subset of the beetle assemblage. This aligns with previous findings showing the effectiveness of yellow PTs for capturing a broad range of beetle species (Vrdoljak and Samways 2012; Cavaletto et al. 2021; Egorov et al. 2024; Kuhn et al. 2024). White bowls formed tighter species clusters, particularly for the “saproxylic” group, suggesting that they sampled a more consistent core assemblage. Further research is required to understand this relationship fully, but this may reflect species attraction to white wavelengths or sensitivity to achromatic contrast (Vrdoljak and Samways 2012; Sukovata et al. 2022). Blue bowls showed moderate species dispersion and partially overlapped with both white and yellow bowls, indicating that they attracted a broad but consistent set of dominant species. These patterns

reflect GLM results, which indicated that blue bowls likely attracted a higher number of dominant species relative to the other colours, but did not influence overall species richness. Furthermore, ISA found statistically significant species associations with each PT colour, showing the importance of using a combination of trap colours (Online Resource 1: Table S3).

Heretofore, no studies have evaluated the effect of IT Bottle Direction on beetle capture rates. Typically, ITs are treated as omnidirectional, with beetles intercepted from all sides but funnelled into a single collector (Bouget et al. 2008; Sverdrup-Thygeson and Birkemoe 2009; Sbaraglia et al. 2025). This approach overlooks potential directional trends in beetle flight behaviour, which could inform species ecology and improve trap design. Existing flight studies predominantly examine the dispersal capabilities of invasive species, revealing that movement is shaped by multiple factors: beetle body mass; wing morphology; sex; life-phase; surrounding temperature; wind; and habitat structure (Evenden et al. 2014; Venn 2016; Keena 2018; Jones et al. 2019). Here we assessed whether IT placement (bottle direction) significantly affected beetle captures, and whether treating each bottle direction as a distinct sample contributes valuable ecological data. We found that IT Direction significantly affected the abundance of the “All Beetles” group only. North-facing bottles (closest to the tree trunk) captured significantly fewer beetles than south and west-facing bottles. Several factors affecting beetle flight may explain this pattern. Microclimatic variation may have had some influence. Many beetles exhibit increased activity in warm, sunlit areas (Koch Widerberg et al. 2012; Horak et al. 2014; Jones et al. 2019; Wijerathna and Evenden 2020; Hannigan et al. 2023). South and west-facing bottles were more exposed to sunlight, which may have stimulated greater beetle flight activity in these warmer air zones. Since ITs were passive, i.e., non-baited, higher capture rates in these directions likely reflect increased beetle movement in these air-zones, rather than true directional preference. Wind direction was likely another important factor. Ireland’s prevailing winds are predominantly south-westerly (Met Eireann n.d.). Therefore, beetles flying downwind or being passively carried by it were more likely to be intercepted by south and west-facing bottles. Surrounding woodland structure also possibly impacted beetle interception. North bottles were possibly obstructed by the FT the trap was hung on, limiting beetle access to the trap from the northern side, and reducing beetle catches. In contrast, south and west-facing bottles were unobstructed. Notably, studies show 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). Beetle behaviour may have also had some influence, with some specimens captured in south and west-facing bottles possibly flying purposely towards the FT for various reasons, e.g., to locate food, mate or oviposition sites (Byers 1999; Evenden et al. 2014; Jones et

al. 2019; Wijerathna and Evenden 2020). Directional effects may also have been driven by a subset of dominant, non-saproxyllic species from the “All Beetles” group, which were more frequently captured in south and west-facing bottles. This would explain the non-significant effects for the “Saproxyllic” group and overall species richness for both groups. While other factors may explain these patterns, a paucity of direct evidence, particularly regarding saproxyllic beetle response to microclimate variation and trap orientation, limits our interpretation and highlights the need for further targeted research.

Across both beetle groups, all IT directions found unique species, relative to the entire IT catch. East-facing bottles contributed the highest proportion of unique capture rates, followed by south, north and west. These results suggest that separating IT bottle samples may reveal subtle ecological patterns, possibly shaped by microclimate, species-specific behaviour, or habitat structure. This highlights the effectiveness of using omnidirectional trap designs to improve species detectability. However, despite each IT direction contributing unique species, considerable species overlap was noted overall across both beetle groups, and multivariate analyses found non-significant differences. This suggests that species captured across the four directions were broadly similar, and observed patterns were ecologically minor or stochastic. Nonetheless, ISA identified two species strongly associated with east and north-facing bottles, which may provide insight into the ecological requirements or flight behaviour of those taxa (Online Resource 1: Table S3).

Beetle Assemblage Correlations

Flight-intercept traps are the most widely used sampling method for woodland-associated and saproxyllic 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. 2008; Sverdrup-Thygeson and Birkemoe 2009). Here, ITs captured a substantial proportion of total beetle abundance and species richness found across both beetle groups. Given their widespread use and apparent effectiveness, we evaluated whether ITs provided a representative characterisation of the local beetle assemblage, compared with ETs and PTs. Specifically, we asked: If ITs were used alone, would key ecological information be missed? Moreover, if resource limitations required omitting a trap type, dropping which trap type would minimise ecological data loss? To answer these questions, Mantel tests were used to assess correlations between the IT beetle assemblage and those of the other trap types. No significant correlations were found between IT and ET assemblages for either beetle group. This is unsurprising given that each trap type targeted different woodland strata and microhabitats, and thus, collected ecologically distinct components of the overall beetle assemblage, i.e., ITs sampled flying beetles in the shrub layer, while ETs targeted specialised,

substrate-associated beetles emerging from grounded dead/decaying wood. This indicates that using ITs alone would have overlooked ecologically distinct taxa targeted by the ETs and highlights that these two trap types are best used in tandem. In contrast, significant, positive correlations were found between IT and PT assemblages for both beetle groups. Notably, this pattern holds true for the “Saproxylic” beetle group. Although PTs are not commonly used to sample saproxylic species, they captured a similar assemblage to that of the widely used ITs. This overlap has important practical implications: where trap simplification is required, PTs could be omitted, provided that ITs are retained. However, while correlated, each trap type captured unique species, and removing any one would reduce the ecological breadth of the sampled assemblage. Therefore, trap selection should balance logistical feasibility with the overarching goal of ecological completeness. Note also that no significant correlations were found between ETs and PTs for either beetle group, reinforcing the importance of including ETs in woodland beetle surveys, particularly when targeting saproxylic species.

Practical Considerations

Ecological sampling methods should be selected primarily for their ability to: a) effectively capture the target insect taxa; and b) address the research questions posed. However, practical and logistical factors must also be considered when designing a sampling strategy (Alinvi et al. 2007; Cohnstaedt et al. 2012; Montgomery et al. 2021; Devi et al. 2025; Hoffmann 2025). All traps were handmade here to reduce costs substantially and allow for the deployment of higher trap numbers. This required considerable time and effort, however. Beyond construction, the time and effort required to deploy and dismantle traps, and collect and sort samples should be considered. Surveyors should first identify which aspects of trap efficacy are most critical for their survey goals before selecting methods accordingly. The relative efficiency scores for trap types used here are given in Table 8.

Table 8 Comparative efficiency measures for each of the three trap types used in the study: flight-intercept (IT), emergence (ET), and pan (PT) traps. Efficiency measures modified from Alinvi et al. 2007

Variable	IT	ET	PT
Time To Create	1	2	3
Cost To Create	1	3	2
Time To Set-Up in Field	2	3	1
Sample Collection and Trap Reset Time	3	1	2
Time to Dismantle in Field	2	3	1
Sensitivity to Surroundings	2	1	3
Laboratory Samples Processing Time	3	1	2
Sum	14	14	14

Methods are ranked, on a per-trap basis (x1 trap), relative to one another, based on the author’s own experience across the sampling season. Low rank (1) corresponds to higher efficiency

Flight-intercept traps were inexpensive and easy to create, took a moderate amount of time to deploy and disassemble, and were not overly sensitive to environmental conditions. Combined with their high sampling efficiency, this makes ITs particularly suitable for long-term site evaluations and native species monitoring. They offer a cost-effective protocol that can be easily replicated every 4-6 years to track temporal changes in beetle assemblages. However, IT sample collection and sorting were the most time-consuming, as four samples were collected per trap, and they captured the highest beetle abundance. Emergence traps were moderately costly and time-consuming to construct. They took the longest to install and dismantle, but once set up, ET samples were the quickest to collect, reset, and sort. They were also the least sensitive trap type to environmental disturbances. Pan traps were relatively inexpensive to make, quick to set up and dismantle, and samples were quick to collect and sort. However, they took the longest to create *per trap* (due to required paint-drying time), and were sensitive to their surroundings. Thus, they were left up for a short period in suitable weather and only reflect a snapshot of beetle activity. While all three trap types had equal total efficiency scores here (Table 8), each had different strengths and weaknesses. When selecting traps, these differences should be weighed against study goals, resources, and constraints.

To further enhance species detection, particularly for rare saproxylic species that may be missed by passive trapping, handsearching is recommended as a complementary technique to our trapping methods. This should involve monthly visits (at least three days each, coinciding with peak activity periods) across the entire field season, where surveyors actively search for beetles in important microhabitats, e.g., tree rot holes, under decaying bark. Handsearching also allows for the collection of both adult and immature beetles. This is important given the limited ecological knowledge of immature beetles in Europe, especially for saproxylic species, despite this being the longest-lived life stage of most species, and the critical importance of knowing larval development sites to accurately classify a species as *truly saproxylic* (Crowe et al. in prep.). Handsearching is intrusive, however, and destroys saproxylic microhabitats that take decades to develop. Its use should, therefore, be carefully justified and limited to experienced surveyors capable of accurately identifying all resulting beetles (including larvae) (Alexander 2004; Nageleisen and Bouget 2009; Alexander 2011; Gobbi et al. 2018; Karpiński et al. 2021; Köhler et al. 2022; Mendicino et al. 2025). Further sampling recommendations are noted in Table 9.

Table 9 Recommendations to enhance future sampling strategies further, along with justifications for this advice

Recommendation	Justification
Begin sampling earlier (April)	To target early emerging species.
Incorporate consecutive sampling years (2-10)	To account for extended developmental periods of saproxylic species within dead/decaying wood and capture temporal changes in beetle assemblages as wood progressively decays.
Use Propylene Glycol as trap preservative	Less toxic to wildlife than Ethylene Glycol and is colourless, possibly reducing visual trapping bias.
Combine all four intercept bottle samples into one	To save time and effort collecting and sorting samples.
Add second collection point below emergence traps to function as pitfalls	May capture a distinct suite of species e.g., those incapable of flight or deterred by light.
Raise emergence traps off the ground	To reduce flooding impacts. In a related study some ETs maintained in the woodland during winter months were effected by severe flooding.

Recommendations are based on the author's own sampling experience

Conclusions and Future Directions

This study presents an effective sampling strategy for woodland-associated and saproxylic beetles, novel for Ireland and Europe. Our results show how trap type and design influence the completeness and composition of sampled beetle assemblages, providing a robust evidence base for efficient and standardised monitoring programmes. These findings will inform future sampling strategies and support the development of conservation tools, such as: a national woody-habitat scorecard for saproxylic beetles; Irish beetle checklists; and the upcoming European saproxylic beetle Red-List.

Overall, our findings indicate that:

1. Trap Type had significant effects on beetle assemblages. Although each trap type had limitations, using complementary methods that targeted different microhabitats was effective. Flight-intercept traps serve as a core sampling method to collect high beetle abundance and species richness. However, they should be supplemented with ETs and PTs to increase the species pool and target saproxylic species specifically.

2. Pan trap colour significantly influenced capture rates, and a combination of blue, white, and yellow bowls proved effective for sampling woodland-associated and saproxylic beetles. Blue bowls were important for collecting a higher beetle abundance. However, all colours contributed unique species and sampled different subsets of the beetle assemblage, reinforcing the strength of using multiple trap colours to maximise sampling coverage. While directional effects were weaker, relative to Trap Type and PT Colour effects, IT Bottle Direction significantly influenced overall beetle abundance, and each bottle direction contributed unique species. These findings emphasise the importance of using multi-directional traps in beetle studies and suggest that incorporating directional data may provide valuable ecological information.
3. In studies where resource limitations require sampling simplification, PTs could be dropped to *minimise* ecological data loss, ensuring ITs are retained. Studies using ITs alone will underrepresent or completely miss some species and, therefore, should be supplemented with other trap types to capture a more representative species list.

Importantly, our findings confirm that every trap type had inherent limitations. Future studies employing one or more of these methods should clearly acknowledge these limitations and the likely gaps in data they produce. Our study also highlights the lack of empirical data on saproxylic responses to microclimate variations and trap orientation. Future studies should, therefore, address these knowledge gaps using targeted research designs. Follow-up studies conducted by the author will compare trapping methods across different Irish woodland types and evaluate the effects of sampling location and surrounding environmental variables on local beetle populations.

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