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RESEARCH ARTICLE

Comparing passive acoustic monitoring bat data from commercial and open-source detectors: Evidence to support best practice

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Email: samperks@connect.glos.ac.uk**Handling Editor:** Rachel Buxton**Abstract**

1. Passive acoustic monitoring (PAM) is an important survey method used to collect data on bat distribution and activity that are needed to underpin conservation and management. The introduction of open-source acoustic recorders at price points considerably lower than those for commercial detectors means PAM is becoming increasingly accessible to practitioners. However, uncertainty regarding recording quality, especially at higher frequencies, makes understanding the comparative performance of commercial and open-source devices imperative.
2. Here, two types of commercial bat detectors: full spectrum (Anabat Swift) and zero-crossing (Anabat Express), and open-source AudioMoth acoustic recorders (configured to use 250kHz (hereafter low) or (384kHz hereafter high) sampling rates) are compared in each of four different habitats: riparian, woodland, wood pasture and arable. In each habitat, comparisons are made using detectors that were spatially co-located and recording on the same nights, such that they had identical opportunity to record the same data. Species accumulation curves were additionally created for each detector type to quantify the combined effects of using multiple detectors, multiple locations per site and multiple temporal replicates.
3. When directly compared, full spectrum commercial detectors outperformed open-source devices (regardless of sampling rate) for many metrics, including for species richness (i.e. the number of species recorded) in all habitats tested. However, the low frequency open-source device performed similarly to the zero-crossing commercial device in quantifying overall bat activity and activity of individual taxa in most habitats. The low frequency open-source unit consistently outperformed the high frequency open-source unit.
4. Commercial detectors accumulated species more quickly, and one detector at one location per site was typically sufficient to record the full species inventory. However, use of multiple open-source devices over a longer period recorded the same species inventory in three of the four habitats.

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5. Practical implication: Although commercial devices remain the gold standard for recording quality, this study shows that less expensive open-source acoustic recorders sampling at low frequency are viable for PAM where the cost of commercial devices is prohibitive. However, it should be noted that longer survey periods or use of multiple units are often required to obtain comparable data.

KEYWORDS

Anabat, AudioMoth, automated detection, bats, bioacoustics, PAM, survey protocol

1 | INTRODUCTION

Despite representing nearly 20% of global mammalian diversity and providing vital ecosystem services, bats, especially nocturnal echolocating microbats, can be difficult to study. The evidence upon which to base conservation and management strategies can thus be limited, which is concerning given that >80% of bat species that have been assessed by the International Union for Conservation of Nature (IUCN) are threatened, declining or listed as data deficient (Festa et al., 2023). As the number and magnitude of the environmental threats facing bat species increase, there is an urgent need to test, evaluate and develop technologies and protocols for the collection of bat data.

Use of passive acoustic monitoring (PAM) to survey bats began in the late 1980s, with full spectrum detectors capable of storing recordings on built-in memory cards for software-supported analysis emerging onto the market in the early 2000s (Zamora-Gutierrez et al., 2021). This expanded detection capability in relation to surveyor-based activity surveys, as PAM approaches had the potential to be scalable, standardisable and cost-efficient, while also being less labour-intensive than direct survey methods (Browning et al., 2017; Gibb et al., 2018). However, recording ultrasonically at high sampling rates captures entire frequency ranges (i.e. full spectrum) and produces large waveform audio (.wav) files. The storage of these files, even temporarily within detectors, was initially often prohibitive (Frick, 2013). To address the needs of practitioners, frequency division and zero-crossing (zc) devices were developed in the 1990s. This provided an interim solution to data storage limitations by reducing the amount of call information that was stored (Agranat, 2013; Corben, 2004), thereby allowing multi-night data collection. More recently, developments in memory cards and recording compression mean that many commercial detectors have reverted to allowing full spectrum recording, either exclusively or as a user-selected option. However, many researchers and practitioners continue to use legacy zero-crossing technology. Commercial units typically use a built-in trigger whereby audio is only recorded if it meets specific ultrasonic parameters consistent with bat echolocation frequencies (Adams et al., 2012; Browning et al., 2017). However, whilst performance, data storage and battery life have evolved as the technology has advanced (Merchant et al., 2015), costs remain a limiting factor for many practitioners, which has hindered the use and scalability of

PAM (Gibb et al., 2018). The introduction of open-source acoustic loggers, such as the AudioMoth (Hill et al., 2017) has created exciting opportunities for researchers and practitioners to access PAM at costs more realistic for conservation organisations (typically costing <10% of commercial detectors and sometimes as little as 1%). Despite the advantages of lower costs, however, several challenges remain. In particular, many researchers have expressed concern that technical limitations with the on-board micro-electromechanical systems (MEMS) microphones could cause detection issues at higher frequencies, thereby impacting recording quality and fidelity in comparison with commercial units (Brinkløv et al., 2023; Gibb et al., 2018; Kunberger & Long, 2023). Poor recording quality can have important implications for data analysis and bat identification, especially for species that echolocate at high frequencies (e.g. horseshoe bats; *Rhinolophus* species) or that produce low energy calls (e.g. long-eared bats; *Plecotus* species; Barré et al., 2019). Initially, AudioMoths could only be configured to record continuously or to use a pre-configured sleep: wake cycle, unless practitioners had the skills necessary to amend underlying coding (Bota et al., 2023; Kunberger & Long, 2023; López-Bosch et al., 2022; Revilla-Martín et al., 2021; Starbuck et al., 2024). A user-friendly frequency trigger for AudioMoth units was developed and released in the configuration application in May 2022 but was initially largely untested.

From a research and practitioner perspective, it is not only the choice of detector that influences data. Survey effort (e.g. number of detectors, number of locations per site, number of temporal replicates) is typically determined by surveyor assessment of habitat suitability. A minimum monitoring period of five nights in suitable weather conditions is often recommended (e.g. Collins, 2023), with more spatial or temporal replicates suggested where habitat quality is adjudged to be high (e.g. riparian habitats and woodland habitats). The number of locations surveyed within a site and the number of temporal replicates remain subjective decisions that require practitioners to balance data needs against available resources (O'Connell et al., 2024). Ongoing development of PAM technology has resulted in a wide range of survey options, with many of these not empirically tested and best practice not always being clear. Any suggested best practice protocols must also allow for the fact that 'optimisation' of PAM frameworks is not only driven by theoretical considerations but is also cost dependent (Froidevaux et al., 2014). Decisions are thus multifaceted, encompassing detector decisions (type, settings

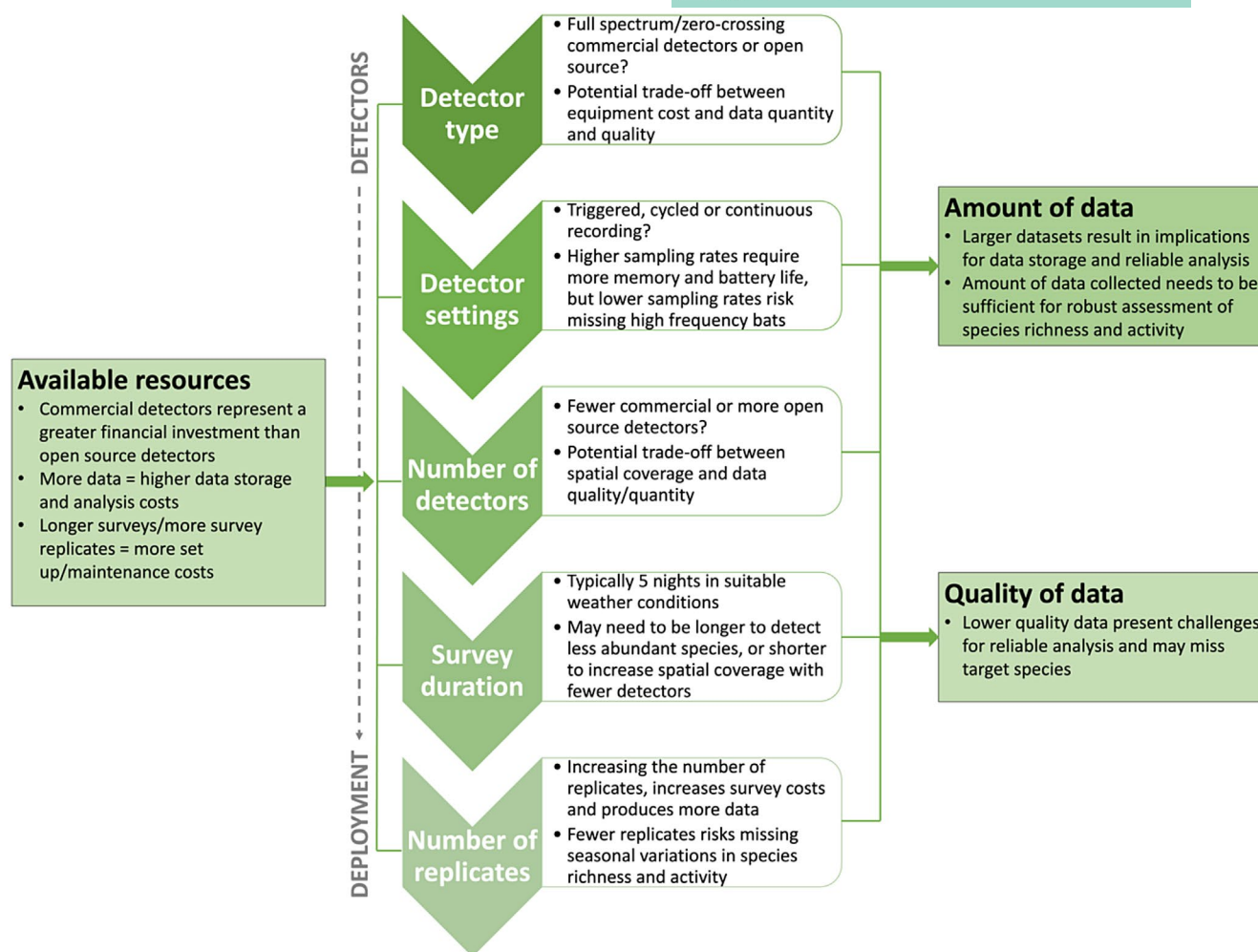


FIGURE 1 Elements of passive acoustic bat survey design that need to be considered when optimising field protocols and sampling schemes using commercial and/or open-source detectors.

and number) and deployment decisions (duration and replicates) (Figure 1).

There has been some previous comparison work on detector types, including between full spectrum and zero-crossing commercial units in America (Adams et al., 2012; Kaiser & O'Keefe, 2015); the former finding full spectrum to outperform zero-crossing and the latter cautioning that the microphone of each detector type could be even more important than the reporting format per se. There have been few commercial versus open-source detector comparisons; however, a recent study conducted by Starbuck et al. (2024) in the United States for a North American bat guild (seven locations at one site, avoiding bat activity hotspots by selecting low quality sites) concluded that there was a trade-off between data quality and cost of data acquisition.

In this study, we empirically compare, for the first time, three types of bat detector: (i) full spectrum commercial units, (ii) zero-crossing (zc) commercial units and (iii) open-source units configured with different sampling rates across a range of temperate lowland habitats that differ in their assessment of quality for bats. We investigate the comparative performance of these detectors

and how the use of multiple detectors at the same site (deployed simultaneously at different parts of the site and/or as successive temporal replicates) affects the data collected. The main bat metrics are species richness (number of species recorded) and bat activity based on the number of bat passes (a bat pass being a sequence of three or more pulses emitted by a bat as it flies past a detector captured within a single recording, as per Starbuck et al. (2024)). Our specific hypotheses are that: (1) the number of bat passes recorded (overall and for specific taxa) will be highest using full spectrum commercial units, intermediate for zero-crossing commercial units and lowest for open-source units; (2) open-source units sampling at higher frequencies will record more bat passes than open-source units sampling at lower frequencies; (3) although bat activity levels and the specific species recorded might vary according to habitat, relative detector performance will remain spatially consistent; (4) species accumulation curves will be detector- and habitat-specific, but by increasing sampling effort for open-source detectors (number of units, duration of survey period), the inherent limitations of open-source units can be overcome. These findings have substantial utility and relevance

for both the research and practitioner communities by supporting the development of enhanced field protocols.

2 | MATERIALS AND METHODS

We recorded bat activity at four sites in Worcestershire, UK, across a 16-week (112 night) period between mid-June and mid-October 2022. All fieldwork was conducted passively with full permission from the respective landowners or managers. Each site supported a different habitat type, ranging from high quality (riparian habitat; woodland habitat) to moderate quality (wood pasture habitat) and low quality (arable habitat). To provide an element of semi-independent spatial replication, each site was split into two geographically separated sub-sites. We surveyed the sites in rotation over successive weeks, whereby data were collected at the first sub-site of each site over survey weeks 1–4, followed by the second sub-site of each site over survey weeks 5–8. To provide temporal replicates, the first sub-site at each site was resurveyed in weeks 9–12, followed by the second sub-site at each site in survey weeks 13–16. In all cases, data were recorded for seven consecutive nights to mitigate the risks of poor weather or equipment failure, but only five nights of data (usually nights 1–5) were carried forward for analysis as per the guidelines in Collins (2023).

2.1 | Detector types and configuration

Detectors from the three main functional types were used: (1) full spectrum commercial units (Anabat Swift, manufactured by Titley Scientific, $n=2$); (2) zero-crossing (zc) commercial units (Anabat Express, Titley Scientific, $n=2$); (3) open-source units (AudioMoth, Open Acoustic Devices; $n=4$). We programmed all detectors to switch on 30min prior to sunset and switch off 30min after sunrise. The Anabat devices were newly acquired specifically for the study, having been factory-calibrated prior to receipt; we configured these to use their standard sampling rate of 500kHz with the on-board trigger activated, such that only sounds that met the pre-programmed criteria based on known parameters for bat calls were recorded. Data were recorded onto San Disk Ultra SD cards (Anabat Swift=64GB+32GB, Anabat Express=32GB). The 32GB secondary SD card in the Anabat Swift devices (where data were recorded in full spectrum) was often required but was always sufficient. In the Anabat Express (where data were recorded in zero-crossing format) a single 32GB SD card was sufficient.

For the AudioMoths, we configured 3 units (v.1.0.0) to use a sampling rate of 250kHz (hereafter Low Frequency AudioMoth; LFAM). These were housed in proprietary cases from the manufacturer and were operational throughout the 16-week survey period. Unlike the Anabat devices, the AudioMoth microphone is recessed within the proprietary case, which may impact its effective directionality. However, all detectors used here were housed in their respective proprietary cases to reflect standard practice. We configured an

additional AudioMoth (v.1.2.0) to use a sampling rate of 384kHz (hereafter High Frequency AudioMoth; HFAM), which was operational for the second temporal replicate only. All AudioMoths were running firmware version 1.7.0. Data were stored on San Disk Ultra microSD cards with card size dependent on sampling rate (LFAM=32GB, HFAM=64GB). At the time of this study, although a frequency trigger had just been launched, this was untested. As the purpose of this research was to compare device performance rather than test the triggers, the units were configured to record all sounds within a pre-determined sleep: wake cycle. To facilitate storing seven nights of data, as would be typically needed within practitioner contexts, we configured the LFAMs to record on a 5-s wake, 15-s sleep cycle, for the first replicate at all sites. For the second replicates, when nights were longer later in the season, we configured the LFAMs on a 5-s wake, 25-s sleep cycle. The HFAM added for the second replicate was configured on a 5-s wake, 20-s sleep cycle.

2.2 | Detector deployment

To enable a direct comparison between detectors, we installed a central 'detector cluster' near the centre of each of the eight sub-sites. This was chosen subjectively based on site geography and to maximise the likelihood of recording bats (for example, in a clearing at woodland sub-sites, along a hedge line at the arable sub-sites). The detector cluster comprised one of each detector type (replicate one=Anabat Swift, Anabat Express, LFAM; replicate two=Anabat Swift, Anabat Express, LFAM, HFAM). In non-linear habitats (woodland, wood pasture, arable), four additional locations were randomly selected relative to the central detector cluster, each of which was randomly allocated a single additional detector from the remaining pool: one Anabat Swift, one Anabat Express and two LFAMs. These additional locations were randomised in terms of direction and distance from the detector cluster, while ensuring that the minimum inter-detector distance was 200m to avoid spatial pseudoreplication. This distance was adopted based on advice that the commercial detectors used in this study may detect lower frequency bat calls from a distance of up to 100m (Titley Scientific, 2025). A similar process was used in the linear riparian sub-sites, whereby the additional locations were situated either upstream or downstream of the central detector cluster, with distances (but not bearings) randomly determined as for non-linear habitats (Figure 2). Regardless of location or detector type, we affixed all units to suitable features, usually trees, shrubs or fence posts, typically 2m above the ground (exceptionally at a minimum height of 1m where they overlooked lower-lying ground), and with the microphone oriented towards open space.

2.3 | Data processing

To remove recordings that were clearly out of bat call range, we used the broad frequency filter 'all bats' in Anabat Insight to delete

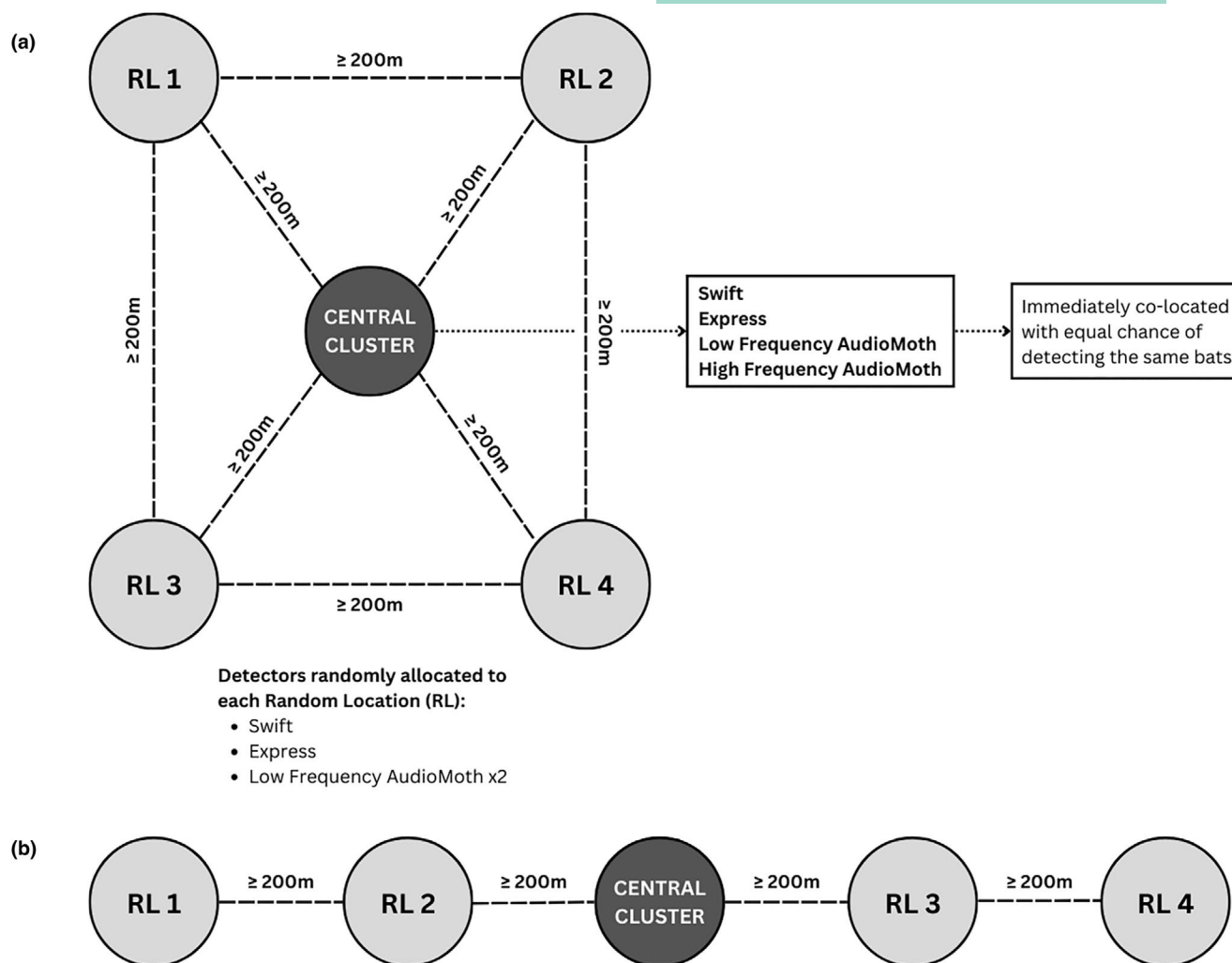


FIGURE 2 Detector deployment within each sub-site for (a) non-linear habitats (woodland, wood pasture, arable) and (b) the linear habitat (riparian).

recordings <4 kHz or >300 kHz. This was especially necessary for AudioMoth recordings as lack of an on-board trigger on these units meant that all sounds were recorded during wake periods. We used the Bats of Europe auto-ID classifier in Kaleidoscope Pro (v. 5.4.0) to classify each recording. Because this classifier was only able to identify a single species per recording, each recording (minimum duration for Anabat devices = 2 s, uniform duration for AudioMoth devices = 5 s) became synonymous with a bat pass, such that the number of recordings per detector per night was a measure of bat activity as recorded by that detector at that location. To minimise false positives during the identification process, we followed the recommendation of Barré et al. (2019) that only classifications with a match ratio of ≥ 0.5 (often treated as analogous to a confidence score of $\geq 50\%$; Braun de Torrez et al., 2017; Springall et al., 2019; Smith et al., 2021; Taillie et al., 2021) should be retained; manual auditing of a random subset of recordings was also undertaken as part of data cleaning, as described below.

Once we had classified recordings to species, and any recordings with a match ratio <0.5 had been removed, some additional

data cleaning was undertaken. First, taxa challenging to differentiate acoustically to species level were grouped: Brandt's bat (*Myotis brandtii*) and whiskered bat (*Myotis mystacinus*) were combined; grey long-eared bat (*Plecotus austriacus*), which is scarce and largely confined to regions outside the study area (Crawley et al., 2020), was reclassified as brown long-eared bat (*Plecotus auritus*). Second, the automated classifications of a random subset of recordings from each species/group were manually audited to verify species identifications. All 56 recordings classified as greater horseshoe bat (*Rhinolophus ferrumequinum*) were removed because none of the audited files had been auto-classified correctly (in all cases, non-bat pulses of the correct frequency had been misclassified). Adopting a cautious approach also meant that all recordings classified as Alcaethoe bat (*Myotis alcathoe*) ($n = 2$), Bechstein's bat (*Myotis bechsteinii*) ($n = 146$) and Nathusius' pipistrelle (*Pipistrellus nathusii*) ($n = 322$) were deleted. The rationale for this was insufficient confidence that these species had been classified correctly, especially given their distribution in relation to the study area and/or because there were too few recordings for

meaningful statistical analysis once the distribution of recordings relative to detector type, habitat, sub-site and temporal replicate was considered. No substantive concerns in the auto-ID classifications of any other species were raised, and no auto-IDs were subjectively changed.

2.4 | Statistical analysis

All analyses were carried out in R 4.2.2 (R Core Team, 2022). To test whether the different detector types in the spatially co-located central cluster differed in performance, we used Friedman tests to compare richness (number of species recorded), overall activity (regardless of taxonomy) and activity of specific taxa. For each bat variable (richness or activity), separate tests were performed for each of the four sites/habitats (with data from both temporal replicates and both sub-sites being pooled at site/habitat level). This allowed for the potential influence of habitat mediating inter-detector differences. The rationale for using Friedman tests was that there was one unit per detector type mounted immediately adjacent on the same single support (tree or fence post) on the same nights, such that they had identical opportunity to record the same bat data. The data thus fitted a repeated-measures framework as they were not independent. Friedman tests were more appropriate than repeated-measures ANOVAs because the data were counts (number of species; number of bat passes) rather than being ratio. We followed each Friedman test with a series of paired Wilcoxon tests for post hoc analysis; these were Bonferroni-corrected to allow for family-wise error. To conduct meaningful statistical analysis on specific taxa with comparatively few records, we grouped all classifications in the genus *Myotis* into a single taxonomic group at genus level and are henceforth referred to as *Myotis* species. We also took this approach by combining classifications from the genus *Nyctalus* with those of *Serotine* (*Eptesicus serotinus*) to form a single taxonomic group henceforth referred to as *Nyctalus/Eptesicus* species.

In addition to analysis on the full dataset, we also undertook analysis on two subsets of these data (henceforth temporally restricted datasets). Subset one included only those data recorded by the two Anabat units at times when the LFAM was awake/recording (20 nights of intermittent data per habitat using both sub-sites and both temporal replicates). Subset two included only those data recorded by the Anabats at times when the HFAM was awake/recording (10 nights of intermittent data per habitat using both sub-sites but only the second temporal replicate). Analysis of these subsets was necessary to specifically test to what extent any differences between the AudioMoths and the Anabat devices in the full dataset might be driven by the latter having the ability to record whenever triggered, versus the former only having the ability to record during their wake periods. The requirement for two subsets was driven by the LFAM and HFAM being configured on different sleep: wake cycles, and also the HFAM only being operational for the second temporal replicate.

To consider the effects of detector deployment decisions (use of multiple sub-sites, multiple detectors per sub-site or multiple temporal replicates) on the species richness recorded in different habitats, and how quickly the full species assemblage was reached, we constructed species accumulation curves using the function *specaccum* in R package *vegan* (Oksanen et al., 2013). This used raw species data rather than species groups used for the Friedman/Wilcoxon tests, and used data from all detectors rather than only the central detector cluster. For the Anabat Swifts and Anabat Expresses, we generated two accumulation curves per habitat using cumulative species richness over successive nights, first using the combined data from two detectors (to simulate a situation when two detectors were deployed at a field site) and second using the mean of the data from two detectors (to simulate a situation when one detector was deployed at a field site). In both cases, data were added cumulatively over successive nights, such that all data from the first sub-site represented nights 1–10, and data from the second sub-site represented nights 11–20. As such, the second replicates at each sub-site commenced on nights 6 and 16, respectively, thus allowing both the effect of a second replicate and a second sub-site to be visualised. The same approach was used for LFAM but using three accumulation curves (one detector, two detectors, three detectors). This approach was not used for the HFAM as only one unit was deployed, which was only operational for the second temporal replicate.

3 | RESULTS

A total of 463,270 recordings made by all the detectors throughout the duration of the study passed the initial 'all bats' filter in Anabat Insight to be carried forward for classification by Kaleidoscope Pro. Of these, 94,306 were classified with a match ratio of ≥ 0.5 ($\geq 50\%$ classifier reported confidence) and were carried forward for statistical analysis. The majority of the classified bat passes were common pipistrelle (*Pipistrellus pipistrellus*) or soprano pipistrelle (*Pipistrellus pygmaeus*) ($n=43,494$ and $29,501$, respectively), followed by *Nyctalus/Eptesicus* species ($n=12,132$).

3.1 | Direct detector comparison using the central detector cluster

The detectors that formed at the central detector cluster at each sub-site recorded a total of 46,428 bat passes: riparian=17,650 (38.0%), woodland=9041 (19.5%), wood pasture=16,537 (35.6%) and arable=3200 (6.9%).

3.1.1 | Full dataset

Analysis of the full dataset using Friedman and Wilcoxon Tests showed significant differences in the species richness and bat activity (both overall and for specific taxonomic groups) among detector

TABLE 1 Friedman test results comparing species richness or bat passes detected by the four detectors (Anabat Swift, Anabat Express, low frequency AudioMoth, high frequency AudioMoth) at the central detector cluster, conducted on the full dataset (df = 3 in all cases).

	Riparian		Woodland		Wood pasture		Arable	
	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Species richness	18.832	<0.001	29.234	<0.001	25.863	<0.001	24.469	<0.001
All bats	20.758	<0.001	30.000	<0.001	28.080	<0.001	25.948	<0.001
Common pipistrelle	19.653	0.001	26.196	<0.001	24.589	<0.001	18.582	0.002
Soprano pipistrelle	19.320	0.001	29.277	<0.001	25.024	<0.001	19.709	0.001
Brown long-eared bat	23.761	<0.001	23.543	<0.001	24.584	<0.001	19.800	0.001
<i>Nyctalus/Eptesicus</i> species	19.129	0.003	27.092	<0.001	22.055	<0.001	13.026	0.032
<i>Myotis</i> species	23.761	0.002	23.761	<0.001	25.710	<0.001	23.062	<0.001
Lesser horseshoe bat	23.548	<0.001	27.710	<0.001	18.31	0.003	12.536	0.040
Barbastelle	2.000	1.000	27.903	<0.001	19.571	0.002	5.667	0.903

types in all four habitats studied (Tables 1 and 2). Across all habitats, there were relatively few differences between the full spectrum commercial Anabat Swift and the zero-crossing commercial Anabat Express (where there were statistically significant differences for specific bat metrics in specific habitats, full spectrum always outperformed zero-crossing: 8.33% of comparisons). The full spectrum Anabat Swift usually performed better than LFAM (63.88% of comparisons) and often better than the HFAM (77.77% of comparisons). The zero-crossing Anabat Express was often better than the HFAM (61.11% of comparisons). When comparing the zero-crossing Anabat Express to the LFAM, performance did not differ in 52.78% of comparisons, with the Express outperforming the LFAM in 47.22% of comparisons. The LFAM often performed better than the HFAM (38.88% of comparisons). The magnitude of the differences in detection for each of the nine bat metrics across each of the four habitats is shown in Figures S1–S5.

3.1.2 | Temporally restricted datasets

Analysis of the two temporally restricted datasets (LFAM subset and HFAM subset) also found significant differences between the bats detected by the different detectors (Table 3). However, in the temporally restricted datasets, although significant differences were found extensively in the HFAM subset, there were comparatively few differences in the LFAM subset. It is also notable that there were fewer significant differences in these subsets than occurred in the analysis of the full dataset (Table 1), both overall and especially for LFAM. The best performing detectors for each of the species/taxonomic groups at each habitat for each subset are summarised in Table 4 and the magnitude of the differences is shown in Figures S1–S5. Of note was the significantly lower species richness recorded by the HFAM in the HFAM subset, which was lower than that recorded by either of the commercial detectors. However, in the LFAM subset, few significant differences were found between the LFAM and the commercial detectors, with the former regularly recording

significantly more bat passes than the Anabat Express in the riparian habitat (Tables 3 and 4).

3.2 | Species accumulation at site level

From the seven detectors that were deployed for the full 20 nights at each site: Anabat Swift ($n = 2$), Anabat Express ($n = 2$) and AudioMoth (LFAM) ($n = 3$), Kaleidoscope Pro classified 11 different species in the recordings from these detectors over the duration of the study.

3.2.1 | Riparian

In the riparian habitat, the combination of two Anabat Swifts had recorded the maximum richness within the first five-night recording period (i.e. first temporal replicate), reaching maximum species richness on night three. A single Anabat Swift took six nights to record the maximum species richness, running into the second temporal replicate at the first sub-site (Figure 3a). Nothing was gained by recording at a second sub-site in either case. Using either one or two Anabat Express detectors recorded the maximum richness of 11 species within the first temporal replicate at the first sub-site (Figure 3b). The three AudioMoths combined required both temporal replicates at the first sub-site to record a lower maximum richness of 10 species, and expanding to a second sub-site did not further improve performance. However, using fewer detectors (1 or 2 units rather than 3) required not only both temporal replicates at the first sub-site, but also both temporal replicates at the second sub-site, and in both cases the maximum recorded species richness was lower than using three AudioMoths. The use of two AudioMoths on average took until night 18 to reach maximum richness, with a mean species richness of $9.66 (\pm 0.33 \text{ SEM})$. The use of a single AudioMoth also took on average until night 18 to record a mean maximum richness of $8.33 (\pm 1.20 \text{ SEM})$ (Figure 3c).

TABLE 2 Comparative performance of Anabat Swift, Anabat Express, low frequency AudioMoth (LFAM) and high frequency AudioMoth (HFAM) across all recordings.

	Express versus Swift	Express versus LFAM	Express versus HFAM	Swift versus LFAM	Swift versus HFAM	LFAM versus HFAM
Species richness	AR: Swift	RI: Express WL: Express AR: Express	ALL HABs: Express	ALL HABs: Swift	ALL HABs: Swift	RI: LFAM WL: LFAM WP: LFAM
All bats		AR: Express	RI: Express WL: Express AR: Express WL: Express AR: Express	RI: Swift WL: Swift AR: Swift RI: Swift AR: Swift	ALL HABs: Swift	RI: LFAM WL: LFAM
Common pipistrelle		AR: Express	RI: Express AR: Express	RI: Swift AR: Swift	RI: Swift WL: Swift AR: Swift	WL: LFAM
Soprano pipistrelle		AR: Express	RI: Express AR: Express	AR: Swift	RI: Swift AR: Swift	RI: LFAM
Brown long-eared bat	AR: Swift	RI: Express WL: Express WP: Express	RI: Express WL: Express WP: Express	WL: Swift WP: Swift AR: Swift	ALL HABs: Swift	RI: LFAM WL: LFAM WP: LFAM
Nyctalus/Eptesicus species	AR: Swift		AR: Express	AR: Swift	AR: Swift	RI: LFAM
Myotis species		ALL HABs: Express	ALL HABs: Express	RI: Swift WP: Swift AR: Swift	ALL HABs: Swift	RI: LFAM WL: LFAM WP: LFAM
Lesser horseshoe bat		RI: Express WL: Express	WL: Express	RI: Swift WL: Swift AR: Swift	ALL HABs: Swift	
Barbastelle		RI: Express WL: Express	WL: Express WP: Express	WL: Swift WP: Swift AR: Swift	WL: Swift WP: Swift	
Overall performance	Swift better 3/36 comparisons (8.33%)	Express better 17/36 comparisons (47.22%)	Express better 22/36 comparisons (61.11%)	Swift better 23/36 comparisons (63.88%)	Swift better 28/36 comparisons (77.77%)	LFAM better 14/36 comparisons (38.88%)

Note: Colour coding (key in column headings) indicates the best performing detector type for each bat variable tested where this is statistically significant (grey = no significant performance difference between detector types). Codes: ALL HABs = all habitats, RI = Riparian, WL = Woodland, WP = Wood Pasture, AR = Arable. Overall performance for each detector pairing is summarised in the final row. The magnitude of the differences and *p*-value details are shown in Figures S1–S5.

TABLE 3 Friedman test results comparing species richness or bat passes detected by the three detectors (Anabat Swift, Anabat Express, AudioMoth), for each of the AudioMoth subsets: low frequency AudioMoth (LFAM) and high frequency AudioMoth (HFAM) (df = 2 in all cases).

	LFAM								HFAM							
	Riparian		Woodland		Wood pasture		Arable		Riparian		Woodland		Wood pasture		Arable	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Species richness	4.831	0.089	7.420	0.025	4.906	0.086	3.397	0.183	10.316	0.006	18.200	<0.001	15.842	<0.001	17.684	<0.001
All bats	29.200	<0.001	24.700	<0.001	25.139	<0.001	15.158	<0.001	14.600	<0.001	2.811	<0.001	14.368	<0.001	15.744	<0.001
Common pipistrelle	22.354	<0.001	15.474	0.003	14.889	0.004	12.329	0.011	9.556	0.042	11.806	1.000	11.706	0.020	8.222	0.082
Soprano pipistrelle	21.641	<0.001	10.839	0.031	20.848	<0.001	4.333	0.573	14.000	0.005	12.560	0.019	10.207	0.043	14.774	0.003
Brown long-eared bat	7.2766	0.158	0.031	1.000	2.711	1.000	INSUFFICIENT DATA	INSUFFICIENT DATA	13.000	0.008	7.189	0.013	8.539	0.098	INSUFFICIENT DATA	INSUFFICIENT DATA
Nyctalus/Eptesicus species	34.816	<0.001	24.514	<0.001	26.000	<0.001	7.404	0.123	8.267	0.016	11.200	0.192	7.294	0.183	9.769	0.038
Myotis species	7.614	0.133	14.358	<0.001	1.793	0.317	1.857	1.000	7.1538	0.028	12.562	0.026	13.862	0.006	7.760	0.103
Lesser horseshoe bat	5.429	0.398	10.511	0.037	9.188	0.071	6.938	0.156	INSUFFICIENT DATA	INSUFFICIENT DATA	11.812	0.013	5.546	0.437	3.500	0.869
Barbastelle	INSUFFICIENT DATA		9.418	0.063	0.696	1.000	INSUFFICIENT DATA	INSUFFICIENT DATA	INSUFFICIENT DATA	INSUFFICIENT DATA	18.200	0.019	5.765	0.392	INSUFFICIENT DATA	INSUFFICIENT DATA

TABLE 4 Comparative performance of Anabat Swift, Anabat Express, low frequency AudioMoth (LFAM) and high frequency AudioMoth (HFAM) for times when AudioMoths were recording only.

	LFAM subset		HFAM subset	
	Express versus Swift	Express versus LFAM	Express versus Swift	Express versus HFAM
Species richness				
All bats		RI: LFAM	ALL HABS: Swift	ALL HABS: Swift
Common pipistrelle		RI: LFAM		WL: Swift
Soprano pipistrelle		RI: LFAM		AR: Swift
Brown long-eared bat				
<i>Nyctalus/Eptesicus</i> species		RI: LFAM WL: LFAM WP: LFAM	RI: Express	RI: Swift AR: Swift WL: Swift AR: Swift
<i>Myotis</i> species				
Lesser horseshoe bat			RI: Express WL: Express WP: Express	WL: Swift WP: Swift
Barbastelle			WL: Express	WL: Swift
Overall performance	No significant differences	LFAM better 6/33 comparisons (18.18%)	Express better 1/32 comparisons (3.13%)	Swift better 14/33 comparisons (42.42%)

Note: Colour coding (key in column headings) indicates the best performing detector type for each bat variable tested where this is statistically significant (grey = no significant performance difference between detector types). Codes: ALL HABS = all habitats, RI = Riparian, WL = Woodland, WP = Wood Pasture, AR = Arable. Overall performance for each detector pairing is summarised in the final row. The magnitude of the differences and *p*-value details are shown in [Figures S1–S5](#).

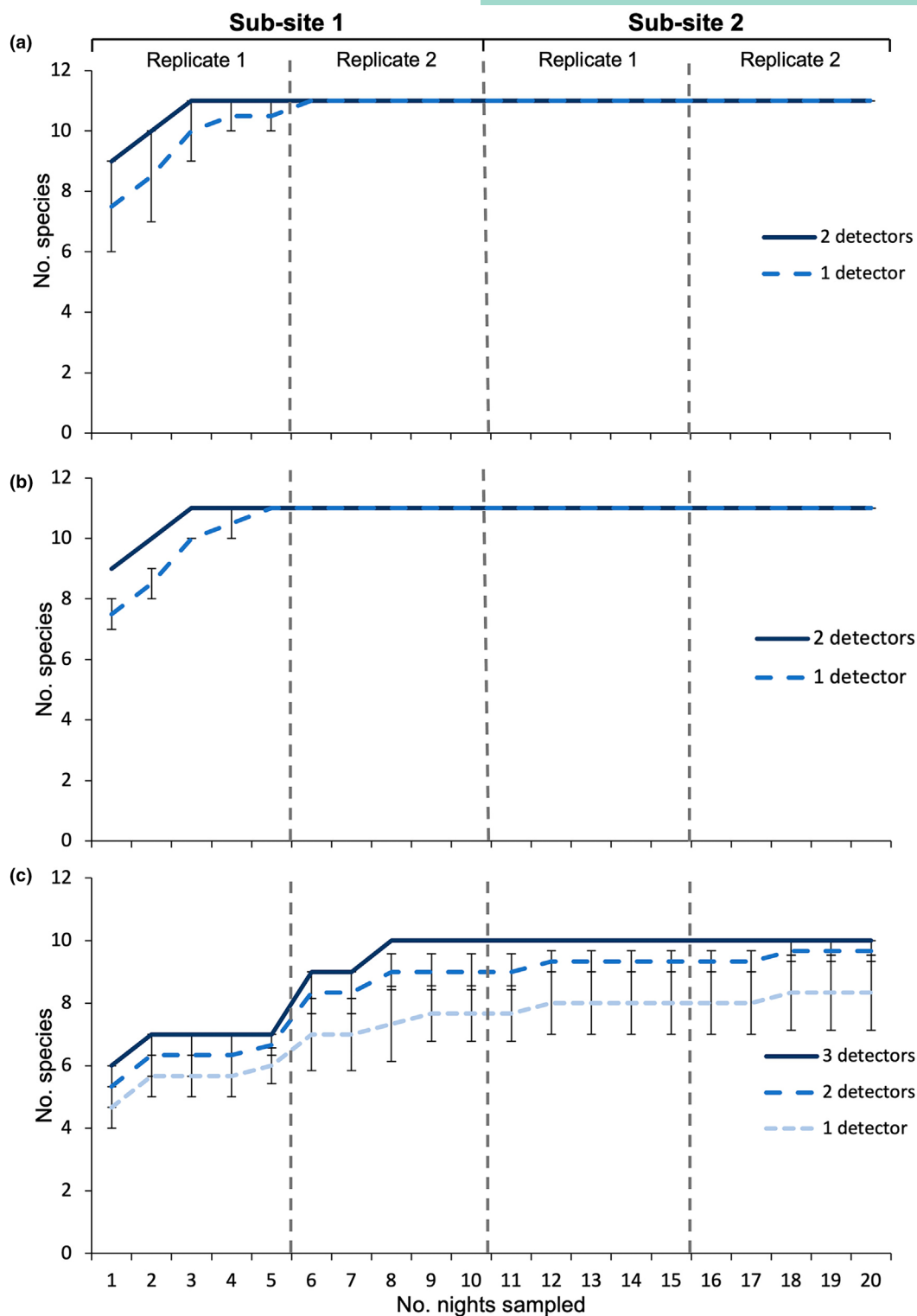


FIGURE 3 Species accumulation curves within riparian habitat for: (a) full spectrum commercial (Anabat Swift), (b) zero-crossing commercial (Anabat Express) and (c) open-source (AudioMoth using 250 kHz sampling rate).

3.2.2 | Woodland

In woodland habitat, the combination of two Anabat Swifts took both temporal replicates at the first sub-site to reach the maximum species richness, recording all 11 species by night seven. Reaching maximum

richness was slower for a single Anabat Swift, taking on average 12 nights (and, therefore, monitoring of the second sub-site) to record the same maximum richness as the two detectors combined (Figure 4a). The temporal efficiency of two detectors versus one was also seen for Anabat Express (Figure 4b). Regardless of the number of detectors

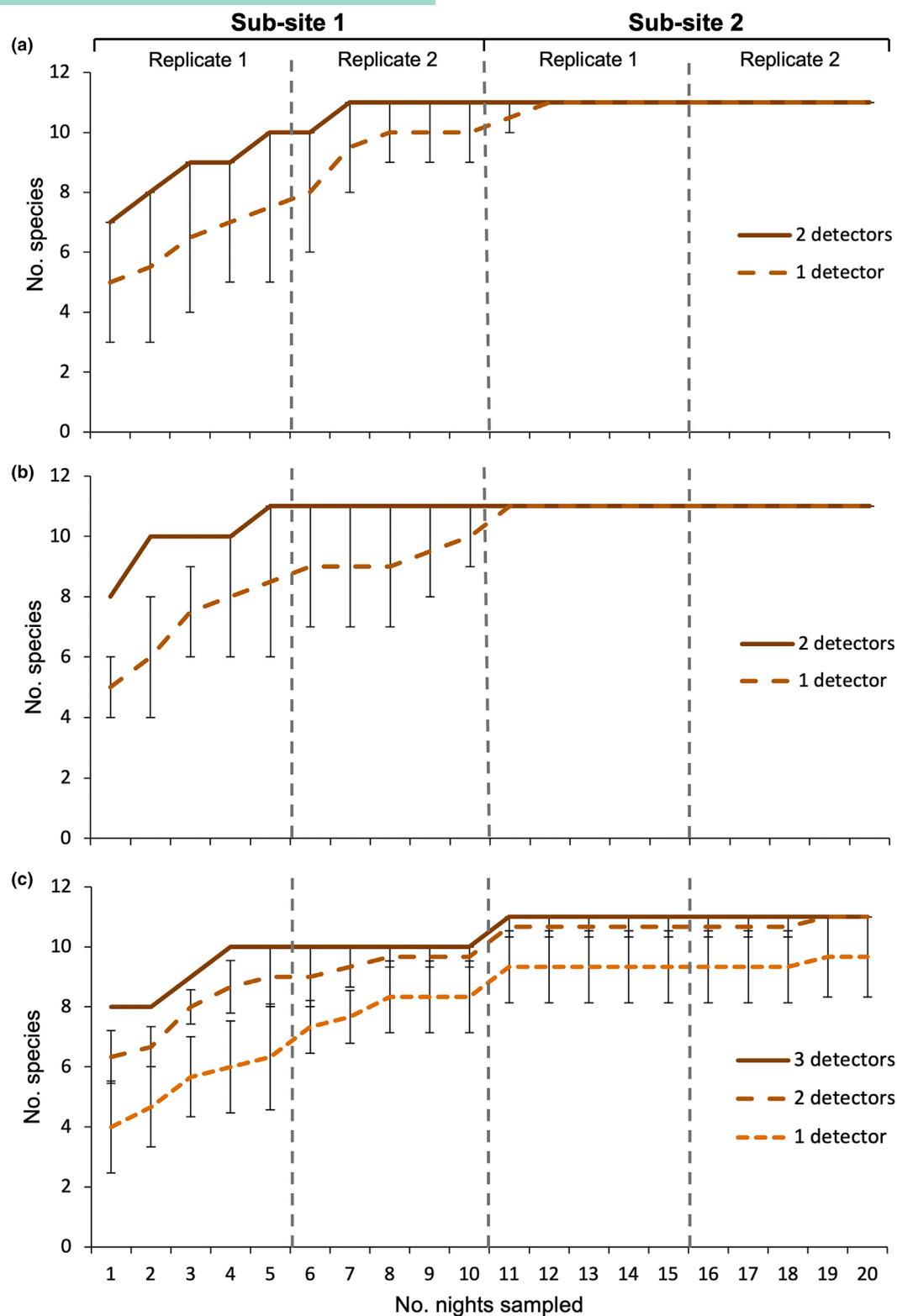


FIGURE 4 Species accumulation curves within woodland habitat for: (a) full spectrum commercial (Anabat Swift), (b) zero-crossing commercial (Anabat Express) and (c) open-source (AudioMoth using 250 kHz sampling rate).

used, the AudioMoths required deployment at both sub-sites to reach maximum richness. The three AudioMoths combined recorded the maximum 11 species by night 11. When using two detectors, it took

19 nights to reach the same species total of 11. Using one detector also took an average of 19 nights for the number of species to peak, but this peak was lower (mean richness = 9.66 ± 1.33 SEM; Figure 4c).

3.2.3 | Wood pasture

In the wood pasture habitat, the use of either one or two Anabat Swift detectors needed both temporal replicates at the first sub-site to reach the maximum richness of 11 species (Figure 5a): nothing was gained by recording at the second sub-site. On the other hand, the combination of two Anabat Express units recorded the same maximum richness more quickly, with the number of species recorded peaking on night three. In this case, though, using a single Anabat Express necessitated both temporal replicates at the first sub-site, with peak richness reached, on average, on night seven (Figure 5b): again, nothing was gained by recording at the second sub-site. The difference between using two or three AudioMoths was negligible, with the maximum richness of 11 species being reached on nights eight and six, respectively, both within the second temporal replicate at the first sub-site (Figure 5c). The use of a single AudioMoth, however, recorded a lower mean maximum richness of 10 species (± 0.58 SEM), which was reached on night 12 using data from both sub-sites.

3.2.4 | Arable

In the arable habitat, use of either one or two Anabat Swift detectors recorded the maximum richness of 11 species within the first temporal replicate of the first sub-site (Figure 6a): nothing was gained by recording at the second sub-site. The Anabat Expresses took comparatively longer; using two detectors reached the same maximum richness on night nine, towards the end of the second temporal replicate at the first sub-site. Recording with one Anabat Express took longer again, with the maximum richness being reached by night 11, on average, requiring recording at both sub-sites (Figure 6b). Only using all three AudioMoths was sufficient to reach the same maximum richness as the Anabat devices, with all 11 species having been recorded by night eight. When using one or two AudioMoth devices, peak species richness was not reached until the second temporal replicate at the second sub-site. Moreover, the mean maximum species richness recorded was lower: 10.66 ± 0.33 SEM by night 16 (2 units) and 8.66 ± 1.22 SEM (one unit) (Figure 6c).

4 | DISCUSSION

The commercial Anabat detectors (Swift and Express) generally outperformed the open-source AudioMoths (LFAM and HFAM), both in terms of the number of species detected (species richness) and overall bat activity regardless of taxa; although the performance of the zero-crossing commercial detector (Anabat Express) was no different to the LFAM in 53% of the bat / habitat combinations tested. This number increased further, to 82%, when analysis was restricted to the time periods in which the AudioMoths were recording. Analysing both the full dataset and restricted subsets was important

to understand the differences in the detectors in both field conditions, as they are likely to be used by practitioners (full dataset) and scientifically under the same conditions (time restricted). Interestingly, the use of AudioMoths did result in the same number of species being detected in woodland and wood pasture habitats as using commercial detectors, but this required the use of multiple detectors and longer sampling periods. In the riparian habitat, the overall species richness recorded was lower using AudioMoths, but the magnitude of the performance difference was reduced when multiple detectors and longer sampling periods were used.

4.1 | Comparative detector performance in relation to habitat

In the analysis of the full dataset, where there were significant differences between detectors (Tables 1 and 2), the Anabat detectors always outperformed the AudioMoths, recording greater species richness and/or higher activity regardless of habitat type. This finding highlights the major disadvantage in configuring the AudioMoths to record on a sleep: wake cycle, as bat activity is inevitably missed when the units are asleep. Across all habitats, this pattern was especially evident for *Myotis* species and brown long-eared bats, which can be classed as short-range echolocators (SRE) (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2014), as detector differences for these species were particularly pronounced (Table 2; Figures S2–S5). In contrast, for *Pipistrellus* species, the zero-crossing commercial Anabat Express and the LFAM were more equally matched in performance, with no significant differences in riparian, woodland or wood pasture habitats (Table 2; Figures S2–S5); in the arable habitat, the Anabat Express significantly outperformed LFAM (Table 2; Figures S2–S5). In the analysis of the temporally restricted subsets, fewer significant differences between the detectors were seen, particularly when comparing the LFAM with the Anabat detectors (Tables 3 and 4), suggesting that at least part of the difference in detection rates was driven by the amount of time the detector could be active rather than inherent technological differences. On some occasions, the LFAM recorded significantly more passes than the zero-crossing Anabat Express in the temporally restricted subset (Table 4). This occurred primarily in riparian habitat (which was the highest quality habitat for bats and had most recordings), but also for *Nyctalus/Eptesicus* species in woodland and wood pasture habitats. Neither of the AudioMoths significantly outperformed the full spectrum Anabat Swift in the subset analysis for any habitat (Table 4). This perhaps emphasises the superior ability of full spectrum detectors (even if open-source) to detect bats relative to zero-crossing detectors (even if commercial), alluded to in the analysis of the full dataset. The general tendency for full spectrum units to outperform zero-crossing units (where data are essentially condensed to a series of time versus frequency dots; Agranat, 2013) agrees with Adams et al. (2012) who tested commercial units in America, reporting that the zero-crossing device typically recorded fewer bats than the full spectrum device. When comparing full spectrum devices in our study (Swift vs. LFAM), the higher quality microphone in the Swift is

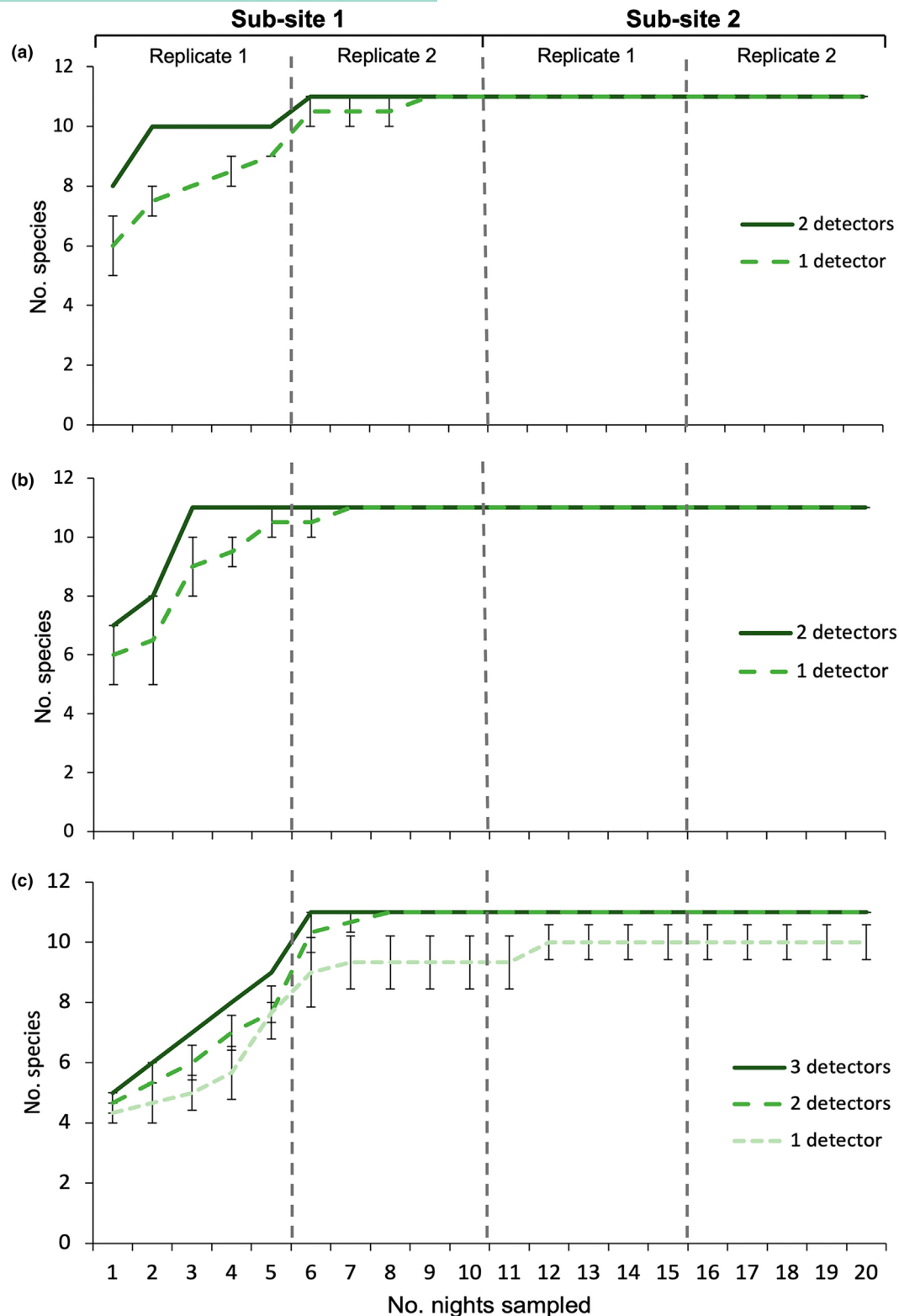


FIGURE 5 Species accumulation curves within wood pasture habitat for: (a) full spectrum commercial (Anabat Swift), (b) zero-crossing commercial (Anabat Express) and (c) open-source (AudioMoth using 250 kHz sampling rate).

likely to be the principal driver behind its performance advantage; indeed, microphones have been previously shown to be more important than whether a detector records in full spectrum or zero-crossing format (Kaiser & O'Keefe, 2015). Indeed, our findings are also consistent

with those of a recent commercial versus open-source detector comparison conducted by Starbuck et al. (2024) in the USA for a North American bat guild, suggesting that this pattern might be generalisable geographically, at least in temperate northern hemisphere ecosystems.

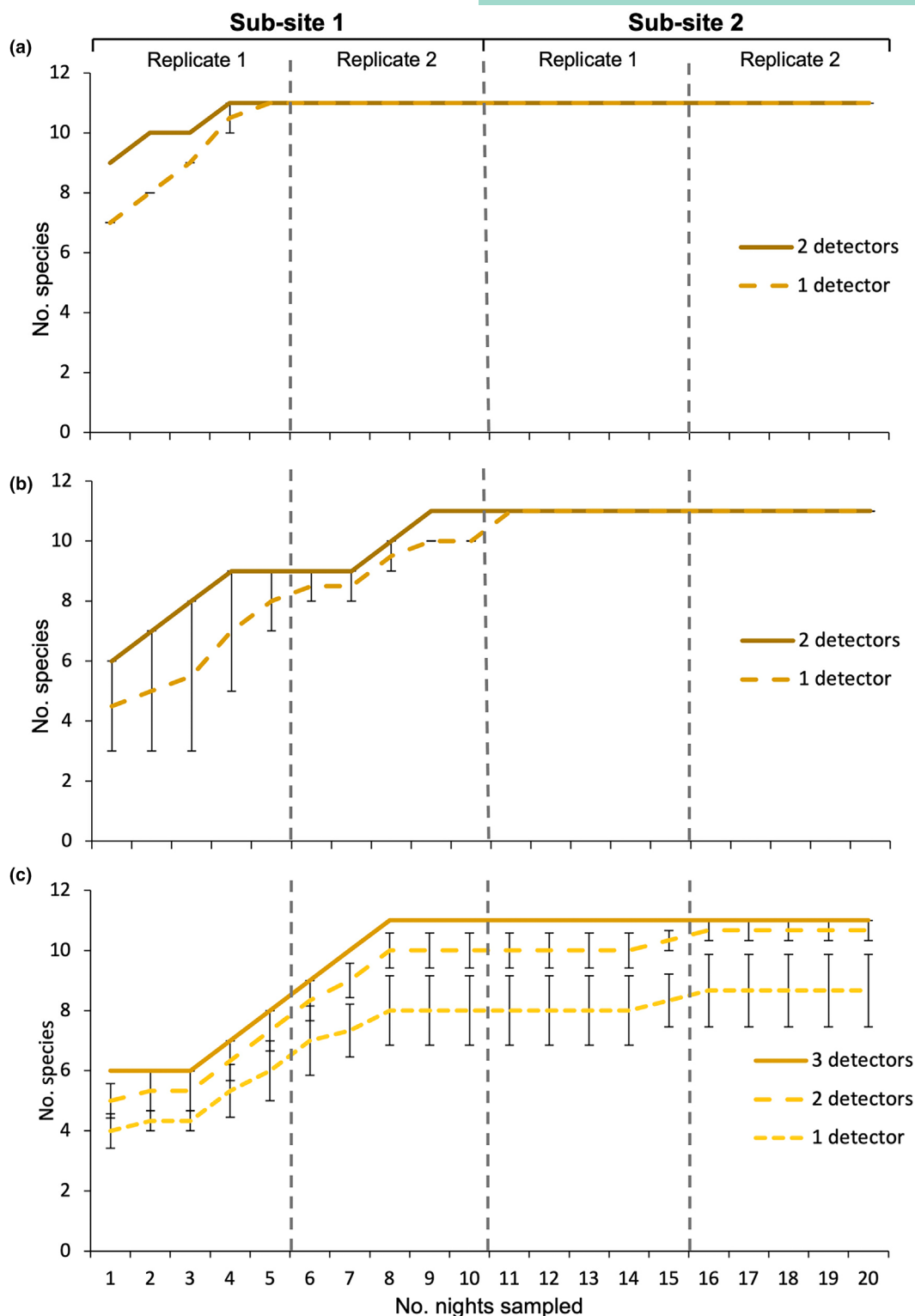


FIGURE 6 Species accumulation curves within arable habitat for: (a) full spectrum commercial (Anabat Swift), (b) zero-crossing commercial (Anabat Express) and (c) open-source (AudioMoth using 250kHz sampling rate).

Where our study adds new information is in the wider range of detector types tested and indicating that the patterns hold across multiple habitat types.

Interestingly, the HFAM was found to underperform in comparison to both commercial Anabat detectors and, in many cases, to the

LFAM. Configuring AudioMoths to use the highest possible (384kHz) sample rate to record bats is recommended by Hill et al. (2019) and has frequently been adopted in previous work using AudioMoth to study bats (e.g. Carvalho et al., 2023; Katunzi et al., 2021; López-Bosch et al., 2022) but is not supported here. The likely explanation

is that whilst configuring AudioMoths to use the highest possible sampling rate can result in high-resolution recordings, particularly for high frequency calls, it additionally generates greater amounts of self-noise from the device's circuitry or components, which may reduce overall recording quality. Increased self-noise can result in calls being overlooked or less confidently identified by a classifier (Brinklöv et al., 2023). The fact that, in our study, the only habitat where there were no differences recorded between LFAM and HFAM was arable, the habitat with substantially less bat activity, provides additional, if tangential, evidence to support this suggestion. A firmware update (version 1.8.0) introducing a frequency trigger for the AudioMoth that could be configured in the user-friendly configuration application (i.e. without needing revision of code by practitioners) was released in May 2022. It was not adopted here owing to the lack of empirical testing (our aim was to compare relative performance of devices in recording bats, not triggers). However, future research should empirically test whether utilising this trigger for AudioMoth yields more comparable results when compared to commercial equipment. If the trigger is effective, the performance difference between (full spectrum) AudioMoths and zero-crossing commercial units is likely to become more pronounced.

To summarise these findings in relation to our initial hypotheses: the first hypothesis, that detector performance would be full spectrum commercial > zero-crossing commercial > open-source, was partly supported; but open-source units were no different to, and indeed sometimes outperformed, zero-crossing commercial units. The second hypothesis, that open-source units sampling at higher frequencies would record more bat passes than open-source units sampling at lower frequencies, was not supported (indeed, the data suggested completely the opposite). The third hypothesis, that relative detector performance would remain spatially consistent, was oversimplistic as, while there were some general patterns that held across all or most habitats, there were also some habitat-specific patterns.

4.2 | Species accumulation

The Anabat detectors recorded all species known to be at each site (and thus for all four habitats studied). In consultancy practitioner terms, therefore, the full species inventory was recorded. When two commercial detectors were used, the maximum accumulation was always reached by the end of the second replicate at the first sub-site (10 nights). This could also typically be achieved by using a single detector; although, in the woodland habitat, the use of a single detector necessitated surveying of the second sub-site for both the Swift and the Express units. This is likely because, in cluttered environments such as woodland, calls are often obscured and higher frequency calls are more easily attenuated (O'Keefe et al., 2014). This finding highlights the need for sufficient spatial coverage in such habitats, even when using commercial detectors.

Although the AudioMoths generally accumulated species more slowly, using multiple detectors had a positive impact. Using three AudioMoths enabled the full species inventory to be recorded within one sub-site, at the wood pasture and arable habitats, and with monitoring of the additional sub-site at the woodland habitat. The lower purchase costs of the AudioMoths make using multiple detectors less of a limitation (Browning et al., 2017); although a slightly longer monitoring period was needed in some cases, overall performance, in terms of recording the presence of species known to be on site, was identical to commercial units for three of the four habitats. The exception was the riparian site, which had the highest levels of overall activity. This was unsurprising, as riparian corridors provide plentiful foraging opportunities for multiple species (Scott et al., 2010; Smith & Racey, 2008). Here, the AudioMoths were not able to record the same species inventory as the commercial detectors, and even the use of 3 units required a second temporal replicate before the (lower) asymptote was reached. More heterogeneous, species-rich habitats with high levels of activity may thus present a challenge for the lower quality MEMS microphone on AudioMoth units. These microphones are hypothesised to have a lower signal-to-noise ratio (also known as noise floor); therefore, environments with high levels of background noise and vocalisations from other species may reduce the ability for specific bat calls to be confidently identified (Gibb et al., 2018; Lapp, 2021). Interestingly, in the woodland habitat, the overall detected level of activity was lower compared to the (theoretically lower quality) wood pasture site. This was shown to impact the effort required to record the maximum species richness, both for AudioMoths and commercial detectors. Bats produce quieter echolocation calls in cluttered environments (Russ, 2012), which can result in fewer detections and give rise to recordings where calls are more challenging to identify. As such, acoustic methods alone are not always sufficient to produce complete species inventories (Lintott et al., 2014).

In summary, our fourth hypothesis: that species accumulation curves will be detector- and habitat-specific; but by increasing sampling effort for open-source detectors (number of units, duration of survey period), the inherent limitations of open-source units can be overcome is largely supported. However, fewer commercial detectors might still produce more comprehensive data than more open-source detectors at busy sites.

4.3 | Implications and recommendations

The findings presented here show that the full spectrum commercial detectors (Anabat Swift) performed most optimally in all four habitats, recording the highest mean species richness and mean numbers of bat passes each night in direct comparisons using the central detector clusters. Moreover, they were seen to accumulate the full species inventory at each site more quickly, and often with the use of fewer units. However, consistent with the findings of Starbuck et al. (2024), AudioMoths provided data of sufficient quality and

quantity to be a viable alternative to commercial units (especially zero-crossing commercial units such as the Anabat Express) where the purchase of commercial equipment is financially prohibitive. Especially with adequate spatial and temporal replicates, using multiple AudioMoths allowed the full species inventory to be recorded as the Anabat Swift in all habitats except riparian. For complex habitats, or those where species richness is anticipated to be high, commercial PAM equipment should still be strongly considered. There are many different contexts under which PAM for bats is undertaken—geographically, environmentally, ecologically and in terms of the aim of the monitoring and the resources available. However, the following guiding principles might be helpful:

1. Where resources are not limiting, use of commercial full spectrum detectors is recommended, especially in high-quality bat habitat (e.g. riparian habitats) and cluttered sites (e.g. woodland habitats). Although outside of the scope of our study, the same is likely to apply to sites with substantive ambient noise (e.g. near roads).
2. Where bat data need to be collected at hard-to-access or remote sites, where visits to replace memory cards and/or batteries become substantive logical considerations, zero-crossing (and, ergo commercial) detectors should be considered. This is because the surveyor time associated with frequent maintenance visits to download data or replace memory cards and batteries contributes to survey costs in ways that are not always considered when simply comparing per unit price (Gibb et al., 2018). The cost associated with storing data is also reduced for data in zero-crossing format.
3. Where detector costs are a limiting factor, the use of open-source detectors is a viable alternative to full spectrum commercial units, especially when multiple units can be used and/or survey durations increased. More specifically, our findings show that using three open-source units provides comparative data on what species are detected relative to one full spectrum commercial unit in most habitats; although in habitats with very high species richness, open-source units might not quite reach the full species inventory.
4. Where a single open-source unit is to be used, it should be appreciated that the data will not be equivalent in quantity or quality to data from a single full spectrum commercial unit or multiple open-source units. However, it is likely to be approximately equal in performance to a single commercial zero-crossing device (our data show that, for some species/habitat combinations, performance is no different; where there are differences these are bidirectional i.e. situations where open-source units outperform zero-crossing commercial devices are balanced by situations where zero-crossing commercial devices outperform open-source units).
5. Our data strongly suggest that configuring open-source AudioMoths with a lower sampling rate better preserves recording quality, potentially by reducing self-noise generated

by device circuitry or components. This is contrary to the recommendation of Hill et al. (2019), which has frequently been adopted (e.g. Carvalho et al., 2023; Katunzi et al., 2021; López-Bosch et al., 2022). Fully understanding the noise generated by different memory cards and how this is impacted by recording at different sampling rates will be of vital importance. In the meantime, we recommend using 250kHz rather than 384kHz and using the fastest memory card possible (class 3) as per the manufacturer guidelines (Open Acoustic Devices, 2024). Empirical testing of the updated AudioMoth firmware with configurable frequency triggers is an important next step to enhance understanding of how these lower cost units compare to the commercial alternatives.

6. As multiple classifiers and pipelines are now available to process acoustic data, we recommend that future work should focus upon gaining an understanding of the reliability of these algorithms and should encompass recordings from different detectors, including open-source units, used in a range of field conditions. The choice of detectors available continues to expand, and thus the potential for variation in component quality, detector cases at ultimately recording quality. The development of open-source devices to synthesise ultrasonic bat calls creates the potential for controlled comparisons which minimise environmental variability. Such approaches may form a valuable next step in ensuring that PAM ultimately produces accurate and reliable data in real-world contexts (Browning et al., 2017; Gibb et al., 2018; Sugai et al., 2019).

Acoustic bat surveys are a vital component in the monitoring and assessment of bat populations and communities, for scientific research (Jones et al., 2013), informing conservation action (Barlow et al., 2015) and to ensure legal compliance under protected species legislation (Collins, 2023). With the expanding availability of acoustic recorders for PAM for bats and other taxa, including birds (Pérez-Granados & Traba, 2021), land mammals (Enari et al., 2019), amphibians (Desjonquères et al., 2020) and insects (Newson et al., 2017), we hope that the findings presented here allow the relative strengths and limitations of commercial and open-source recorders to be better understood.

AUTHOR CONTRIBUTIONS

Samantha J. Perks and Anne E. Goodenough conceived the ideas and designed methodology; Samantha J. Perks collected the data; Samantha J. Perks analysed the data, supported by Anne E. Goodenough; Samantha J. Perks and Anne E. Goodenough led the writing of the manuscript with valuable input from Mark J. O'Connell. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare. Mark J. O'Connell is an Associate Editor of *Ecological Solutions and Evidence*, but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available at: https://github.com/sjperks/ESE_PAM_bats (Perks, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Differences in species richness between detectors. Significant post hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

Figure S2a. Differences in bat passes between detectors. Significant post hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

Figure S2b. Continuation of Figure S2. Significance codes: <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

Figure S3a. Differences in bat passes between detectors. Significant post hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

Figure S3b. Continuation of Figure S3. Significance codes: <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

Figure S4a. Differences in bat passes between detectors. Significant post hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

Figure S4b. Continuation of Figure S4. Significance codes: <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

Figure S5a. Differences in bat passes between detectors. Significant post hoc pairwise Wilcoxon results displayed with codes <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

Figure S5b. Continuation of Figure S5. Significance codes: <0.05(*), <0.01(**), <0.001(***). Plots with reduced saturation indicate no significant overall difference.

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