Bournemouth University

Unlikely Friendships - An Exploratory Review into the Defining Criteria of Associative Behaviour between Vertebrate Species

Masters by Research Thesis Submission

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Abstract

Research on associations between individuals of different species has been conducted worldwide on a plethora of taxa and documented under multiple terminologies. This paper reviews the breadth of this complex social behaviour by collating relevant association papers across all vertebrates that use one or more of the four main terminologies to describe such associations (polyspecific (PSA), heterospecific (HSA), interspecific (ISA), mixed-species (MSA)). Over 400 vertebrate species from 6 phylogenetic classes exhibit a form of association with another species within the 592 papers reviewed.

The definitions of eligible papers were extracted to discover the variety of associations between individuals of different species and how this correlates with the taxon or terminology used. Despite extensive variation and ambiguity across papers, a core set of definition segments has been found to appear in various combinations consistently throughout the dataset.

Both multiple correspondence (MCA) and principal component (PCA) analyses were used to discover trends between the defining criteria/behavioural characteristics recorded and taxa/terminologies. Initial findings highlight a large overlap between taxa/terminologies and their respective definition segments, nevertheless, unique trends were found among primates, birds and polyspecific associations. To mitigate the low explanation of variance and further explore the observed trends, a subsequent targeted dataset was created containing studies focussed on primates in polyspecific associations (Primates:PSA) or birds in mixed-species flocks (Birds:MSA). The separation of defining components in the secondary dataset was seen across all multivariate statistics.

Studies on birds in mixed-species associations (Birds:MSA) were likely to have a nuclear species, unequal benefits between the participating species, a lack of unified territoriality and little aggression towards each other. Primates in polyspecific associations (Primates:PSA) were likely to engage in coordinated activities together such as foraging, resting, alarm response and general interactions for a prolonged duration within proportionally close proximity of each other. Primates:PSA studies often record associative behaviour occurrence beyond the expected ‘chance encounters’ and describe strong seasonality as well as minor

agonistic interactions. Birds:MSA studies recorded fewer defining criteria variables on average than Primates:PSA making true comparison challenging.

A unifying framework for associations between different species regarding the appropriate usage of terminology has been created based on standardised defining criteria. The recommended framework and revised definition aim to be encompassing across all taxa and alleviate researcher ambiguity surrounding associative behaviour to minimise terminology misuse within this field.

Acknowledgements

The dedication of this thesis must be to my supervisors Mandy, Rick and Richard and their unwavering patience for my ever-wavering concentration span.

There is some danger that a symposium on competition which begins with a section on definitions may so irritate later speakers that the whole meeting degenerates into a display of semantics. J. L. Harper (1961)

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1. Introduction

Throughout the animal kingdom there are examples of individuals of different species interacting with each other. In fact, much of life would be impossible without it (Thompson 1999). From pollinators to parasites, predators to prey, most species are bound within an ecological network for food, shelter, competition and reproduction.

Most ecological communities have been described based on their antagonistic interactions i.e. ‘food webs’ and the importance of mutually beneficial interactions are often less strongly embedded in species-interaction frameworks within community (reviewed by Bascompte 2010). Mutualism examples are often dominated by plant-animal networks and rarely consider complex social interactions between vertebrates such as group living or cultural learning (Mönkkönen et al. 1996; Tosh et al. 2007; Ferrari and Chivers 2008; Bascompte 2009).

Research on associations has been largely confined to the parameters of group living within species (Beauchamp 2013; Chapman and Valenta 2015; Guindre-Parker and Rubenstein 2020). The role of associations *between individuals of different* species has often been overlooked due to the comparative scarcity of occurrence (FitzGibbon 1990; Marjolo and Ventura 2004; Heymann 2011; Srinivasan and Quadar 2012; Hanya and Bernard 2021). The lack of focussed, standardised research on the topic has led to vague definition criteria, multiple overlapping terminologies, and conflicting conclusions (Cords 1987; Au 1991; Peres 1991; Desbiez et al. 2010). These inconsistencies are the focus topic of this paper.

1.1. Interactions and Associations

Any interactions between two independent variables will produce an outcome, or reaction. This outcome can be positive, neutral, or negative for either or both parties (Figure 1). In biology, evolutionary drivers propel us to be attracted to the positive interactions we have with our surroundings whilst simultaneously evading negative interactions that may cause harm or death. As life actively seeks out the positive interactions that aid its survival and prevents negative interactions with dangerous repercussions, it begins to find innovative ways to interact more effectively. Such adaptations that interact in a specific way with the environment can become ingrained within a population or species if the behavioural traits promoting such behaviour are inheritable. Alternatively, traditions can develop within a population if there is cultural transmission of behaviours between individuals. (Thompson 1999).

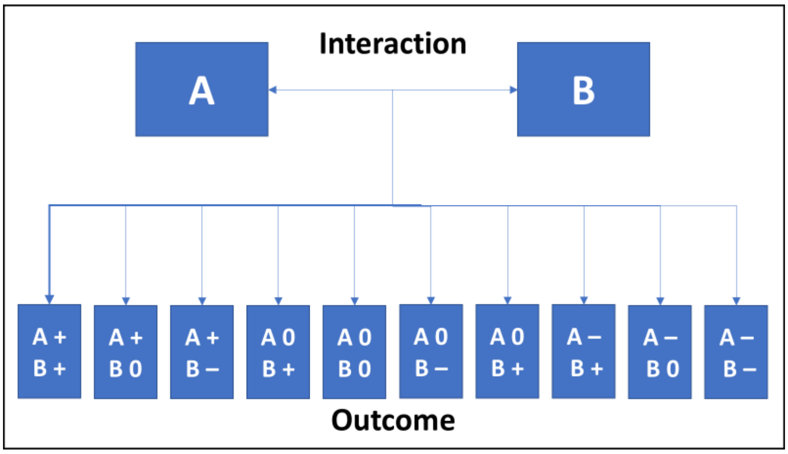


Figure 1: Interaction flowchart showing all the possible outcomes for two individuals. + = positive outcome, - = negative outcome, 0 = neutral outcome.

Due to the vast majority of life having the same fundamental needs for survival, we see similar convergent adaptations appear throughout a plethora of species primarily centred around predation, disease avoidance, reproduction and foraging efficiency (Losos 2011). When an interaction is consistently positive, it becomes somewhat habitual and the individual(s) will routinely pursue this interaction at a rate above that of random encounters. Once this behaviour has become predictable between the two interacting parties, it can be considered to be an association (Greeno 1970). Some species have found an increased number of positive interactions conducive to survival as a result of prolonged sustained association so have adapted to group living (Rubenstein 1978).

1.2. Associations between Individuals within the Same Species

For this paper, we refer to group living as prolonged associations between multiple individuals. They can include:

- Temporary associations – An unrepeated association for a period of time *(such as a temporary bachelor group of unflanged male orangutans (Reukauf et al. 2019))*

- Intermittent associations – An association that exists during certain times of the day or year *(such as protective nesting associations in birds (Quinn and Ueta 2008))*
- Permanent associations – An unceasing association regardless of temporal or seasonal changes *(many species such as monkeys, wolves, hyenas, and dolphin pods (Krause et al. 2002))*

Group living unremittingly operates on a delicate balance between costs and benefits (Krause et al. 2002; Table 1). Competitive intraspecific interactions are associated with costs for an individual that can threaten reproductive likelihood, energy demands and resource availability - especially in groups with strong social hierarchies. Sharing mates and common resources can lead to some weaker individuals being forced to expend more energy searching for enough resources to survive (Markham and Gesquiere 2017).

Table 1: Cost and benefits for associations among individuals of the same species.

	Benefit	Cost	Refs
Foraging/ feeding	● Increased foraging efficiency ● Increased likelihood of monopolisation	● Larger food source needed ● Unequal food proportion ● Kleptoparasitism	3, 5, 6, 7, 8
Safety/ security	● Risk dilution (selfish herd) ● Predator deterrence ● Improved threat detection ● Group confusion tactics	● More detectable	3, 6, 9, 10
Reproduction	● Proximity ● Energy saving ● Multiple mate choice ● Sharing of parenting resources	● Competition ● Mating repression ● Limited genetic variation ● Coercion of females by males	3, 4, 11
Temperature	● Social thermoregulation		1, 2
Social	● Well-being ● Knowledge acquisition ● Alloparental care ● cooperation against competitors	● Disease/ parasite transmission ● Inequality in hierarchy	6, 7, 12
Disease transmission	● Host resistance to pathogen infection ● Reduced fitness impacts	● Increased exposure to pathogen/parasite	13, 14, 15

1- Eppley et al. 2017, 2- McFarland et al. 2019, 3- Alexander 1974, 4- Muller et al. 2011, 5- Stacey 1986, 6- Rubenstein 1978, 7- Brown 1988, 8- McCrate and Uetz 2010, 9- Hamilton 1971, 10- Landeau and Terborgh 1986, 11- Markham and Gesquiere 2017, 12- O'Brien 1991, 13- Côté and Poulinb 1995, 14- Kappeler et al. 2015, 15- Ezenwa et al. 2016.

Nevertheless, despite some potential inequality in benefits and costs between individuals, when we look at the group as a singular entity we almost always see an overall gain that drives and wills this adaptation on (Guindre-Parker and Rubenstein 2020). Individuals will periodically be willing to take a slight loss if it is for 'the greater good', i.e. if their sacrifice will result in a prospective gain for themselves or their kin. This is one of the reasons that the most common type of group living witnessed in the natural world is family units (Krause et al. 2002).

1.3. Associations between Individuals of Different Species

Associations that occur among individuals of different species are far rarer (Peres 1991; Taylor and Skinner 2000). They not only have to optimise the delicate cost-benefit equilibrium of usual monospecific groups, but also manoeuvre their way around a plethora of additional complications that arise from being genetically, behaviourally, and biologically disparate (Table 2). They must achieve a sustainable association with species that, in many cases, would normally be considered competitors due to common resources or predators (Schoener 1990; Keddy 2001). Despite the odds, we continue to see this phenomenon emerge sporadically throughout the natural world. Different species with vastly varying degrees of similarities have been found to coexist together in close proximity for extended periods of time. They are often observed repeatedly engaging in positive or neutral interactions with benefits for at least one party at a rate that is significantly above a chance occurrence (Waser 1984; Mönkkönen et al. 1996; Li et al. 2010; Cords and Würsig 2014).

Table 2: Cost and benefits for associations among individuals from different species.

	Benefit	Cost	Refs
Protection from predators	- Risk dilution - Predator deterrence - Improved detection - Combined defence strategies e.g. mobbing	- Combined predator risk	1, 2, 3, 4
Warning/ Lookout	- More eyes and ears - Combined predator detection strategies e.g. sentinels - Increased dispersion capabilities	- Different predators - Inability to recognise the other species warning calls - Energy wasted from false and premature alarms	1, 2, 3, 4, 7
Increased group size	- Helps with the mentioned benefits	- More visible - More resources needed (food, territory…)	3, 4
Food	- Food detection increase - Combined hunting/ foraging efficiency - Monopolisation of a food source - Less feeding competition if diets are different	- Increased total food consumption - Different dietary requirements - Aggression over valuable foods	1, 2, 3, 4, 7, 8
Utilising habitat	- Shared territories reduces space needed - Can cover larger home ranges	- Stretches limited resources too fine	4, 9
Education	- Possible information transfer	- Knowledge subjective to species - Use the education to outcompete	2, 4, 10
Social	- Increased social interactions - Different species unaffected by kin selection/ mate access	- Increased possibilities of agonistic interactions	4, 5, 6, 8, 11

1- Terborgh 1990, 2- Rehg 2017, 3- Goodale et al. 2020, 4- Stensland et al. 2003, 5- Farine et al. 2012, 6- Baraff and Asmutis-Silvia 1998, 7- Cords 1987, 8- Buchanan-Smith 1999, 9- Gautier-Hion et al. 1983, 10- Podolsky 1990, 11- van Lawick-Goodall 1968.

In spite of the similar fundamental theme within these associations among individuals of different species, there are also numerous disparities. Many appear to be purely 'tolerating' the other for self-gain when needed - environmental pressure perhaps forcing further towards a necessary truce (Guindre-Parker and Rubenstein 2020). They call upon the alliance only when they need the specific benefit and go their separate ways once fulfilled. This temporary association can be witnessed in species such as the Badger *(Taxidea taxus)* and the Coyote *(Canis latrans)*. Their hunting strategies seem to complement each other whilst working together in a hunting association, however the interaction ceases after completion of the hunt (Minta et al. 1992; Thornton et al. 2018).

Others are seemingly inseparable. Some primate species such as *Callitrichines* form extremely stable associations with some species. Peres (1992) observed *Saguinus fuscicollis avilapiresi* (Saddle-back tamarin) and *Saguinus mystax pileatus* (red-capped tamarin), spending up to 98% of their time in active association with one another. They become an integrated unit; sharing territory and resources that they collectively defend from inter-troop competition as well as responding to each other's calls. They share intimate social behaviours with one another that are usually exclusively found in single-species groups such as grooming and playing (Heymann and Sicchar Valdez 1988; Heymann and Buchanan-Smith 2000; De Carvalho et al. 2017).

There are groups that form a bond with just one other species (Rasa 1983; Newton 1989; Thornton et al. 2018), as well as groups that comprise of a bountiful abundance of species (Au 1991; Sazima et al. 2007; Haugaasen and Peres 2009; Shridar and Shanker 2014). Famously noted by Alfred Russel Wallace in 1869, high species diversity is particularly prevalent in tropical birds. Some flocks have been documented to reach an abundance level of over 80 species (Munn 1985).

1.4. Association Terminology

Over the years, many different words to describe this behaviour between species have arisen. The terminologies have fluctuating popularity over time, location, and taxa. This has reduced the clarity and sanctity of not only the definitions themselves but also the differences between them. What is left is a muddied collection of vague definitions.

This paper focuses on reviewing and understanding the most common four terminologies:

- Polyspecific associations
- Mixed species associations/flocks
- Interspecific associations
- Heterospecific associations

These terms are the only terms used to describe this behaviour in the literature search other than extremely infrequent deviations such as foraging associations that are negligible. They relate to studies that, initially at least, seem to describe almost identical interactive behaviours between individuals of different species but fail to use the same terminology. Chapman and Chapman (1996), Struhsaker (1981), and Hayashi (1975) all studied associations of the same species in the same location (Kibale Forest, Uganda) yet all use different terminologies in the titles of their articles. Whilst on the other hand, there are studies which observe species displaying different extremities of this umbrella behaviour categorised under the same one name. Sporadic feeding associations between mammals and complex social tamarin groups are bracketed together under 'interspecific associations' (Haugaasen and Peres 2009; Desbiez et al. 2010).

1.5. The Importance of a Name

The importance of a name should not be underestimated. According to formal logic, definitions must be encompassing enough to capture the essential attributes of the thing described but narrow enough to discriminate between alternative things (Copi et al. 2016). Without clear, logic-based definitions people will create their own defining criteria which are subjective and incomparable as they are based on personal knowledge and research. Furthermore, if there is no universally accepted definition the studies become unfalsifiable leading to gross over- or under-representation of the behaviour. Many may also be mis-defined as a different behaviour resulting in other definitions becoming unclear as well (Vogel and Ingram 1993).

As documented in Table 3, many researchers studying associations between species have expressed their acknowledgement of confusion and vagueness around these definitions (Macdonald and Henderson 1977; Morse 1977; Pook and Pook 1982; Cords 1987; Terborgh 1990; Baraff & Asmutis-Silvia 1998; Stensland et al. 2003; Quérouil et al. 2008; Desbiez et al. 2010) highlighting the inconsistency of sampling methods (Peres 1991; Srinivasan and Quadar 2012; Shridar et al. 2013) and lack of quantitative data (Harrison 1979; Aronson and

Sanderson 1987; Mitani 1991). Most are also in agreement that this topic is relatively understudied (Noe and Bshary 1997; Marjolo and Ventura 2004; Hanya and Bernard 2021), and some have even urged within their papers for the terminologies to be redefined (Dobson 2018). However, despite an awareness of ambiguous definitions and the problems that can arise in studies as a result, no research paper I have found has solely focussed on rectifying the issue. Therefore, this uncertainty in definitions will be the predominant aim of this paper.

Table 3: Quotations from researchers documenting the confusion and ambiguity when defining associative behaviour between two or more different species.

Citation	Taxon	Quote
Terborgh 1990	Inter-order	Although numerous adaptive advantages for mixed foraging parties have been suggested, it has been notoriously difficult to quantify potential advantages in the case of particular types of mixed troops, flocks, schools, or herds. We are thus restricted to studying proximate manifestations rather than the ultimate causes of the phenomenon of mixed groups.
Stensland et al. 2003	Inter-order	A definition of mixed species associations in the literature is often lacking or very broad, making it hard to compare different studies. Mixed species groups have been described for a lot of species but detailed behavioural studies are rare except in primates.
Morse 1977	Inter-order	By this point it should be clear that it is difficult to draw a precise line between the groups discussed here and a wide range of commensal relationships.
Au 1991	Inter-order	The specific interactions involved are not well understood, even though field observations have been intensive in some cases.
Baraff & Asmutis-Silvia 1998	Marine Mammals	The nature of these associations is not always clear.
Struhsaker 1981	Primates	Definitions of primate polyspecific associations in the literature are either lacking or so broad that it is often difficult to make valid comparisons of the available data.
Mitani 1991	Primates	Hypothesis tend to be anecdotal.
Pook and Pook 1982	Primates	References are usually brief and little distinction drawn.
Noe and Bshary 1997	Primates	Hard evidence is scarce.
Macdonald and Henderson 1977	Birds	This variation makes it difficult to devise a general hypothesis to explain the existence of mixed species flocks.
Mönkkönen et al. 1996	Birds	Next to nothing is known about how positive interactions may influence species distributions within or among communities.

Aronson and Sanderson 1987	Fish	Although there are numerous accounts of heterospecific foraging by carnivorous fishes, few quantitative data are available on the costs and benefits to individuals.
Srinivasan and Quadar 2012	Inter-order	The theoretical framework of cost and benefit in multi-species groups has not been explored using formal mathematical models.
Cords 1987	Primates	Some of these reports lack conviction.
Heymann 2011	Primates	There are still very few studies that have analysed the mechanisms of group coordination in mixed-species groups.
Cords and Würsig 2014	Inter-order	Comparatively little is known about such proximate mechanisms in comparison to adaptive function.
Hanya and Bernard 2021	Primates	We need more studies of interspecific encounters to understand the lack of polyspecific associations in Asia.
Ferrari and Chivers 2008	Amphibians	Moreover, few studies have considered cross-species learning among members of mixed-species assemblages.
Karplus et al. 2007	Fish	Relatively few studies have addressed the question of interspecific social learning in fishes, including foraging behaviour.
Quérouil et al. 2008	Marine Mammals	Few studies have focused on the ecology of mixed-species aggregations in the family Delphinidae and their function is still not well understood.
Srinivasan 2008	Birds	Further, the nature of, and the mechanisms underlying interspecific associations in mixed-species flocks are poorly understood, and have received mainly theoretical attention.
Peres 1991	Primates	Sampling methods determining these estimates are inconsistent between studies.
Harrison 1979	Inter-order	Are largely anecdotal.
Desbiez et al. 2010	Inter-order	The definition of mixed species associations in the literature is often very broad or even lacking.
Farine et al. 2012	Birds	Literature syntheses make it clear that while these hypotheses are important, much about mixed-species groups remains unexplained.
Haugaasen and Peres 2008	Inter-order	In contrast, little information exists on associations between primates and other mammals, and the majority of the observations refer to brief encounters or interactions rather than prolonged associations.
Marjolo and Ventura 2004	Inter-order	The primate order is not well represented by studies on this subject, with scarce data concentrated on few species.

2. Aim and Objectives

The aim of this study is to create a clearer understanding of the variety of associations between species and discover key discrepancies which can be implemented within defining criteria to construct distinct, universal, standardised terminology relating to multi-species associative behaviour.

Therefore, this study will:

- Review existing literature within this topic to establish the breath of associative behaviour between vertebrates.
- Systematically extract what the researchers involved considered to be the essential criteria when defining this behaviour both through words and methodology.
- Analyse the isolated definition segments to identify any trends that might suggest the segregation or collation of this behaviour and its respective terminologies.
- Create clear, encompassing definitions for this behaviour with a precise set of standardised defining criteria so behaviours can be identified, categorised, and studied more accurately in the future.

3. Method

3.1. Study Selection and Assessment

3.1.1. Data Collection

An exhaustive literature search was conducted to maximise the number of descriptions of multi-species associative behaviour found. Given its preference within the scientific community, the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) framework was followed (Moher et al. 2010; Figure 2). A primary literature search was run using Google Scholar and Web of Science. Each of the four focus terminologies (polyspecific associations, interspecific associations, heterospecific associations, mixed species associations) were searched for in the title or abstract using advanced searches. A scan of the titles acted as an initial elimination stage, bypassing any studies that seemed to be out of scope. The abstracts of available papers were reviewed and, if they were considered relevant, were subsequently read thoroughly and documented. Important information was recorded including location, habitat, data type and taxa (to species level where possible; Table 4). A subsidiary data search was conducted by using the bibliographies of papers that passed the screening and eligibility stage until there were repeatedly no new relevant papers found.

Flora and invertebrates were excluded from this study due to the vast differences in researcher methods and behavioural analyses. Material used was restricted to peer reviewed scientific articles, but both primary research and review articles were included.

3.1.2. First Analysis Dataset

A data sheet was compiled containing: a breakdown of all possible components of multi-species associative behaviour; terminology used; drivers; and observed related behaviours between species (Table 5). These data were further split into whether the mentioned behaviour components were found in the context of a definition for multi-species associative behaviour or whether it was observed during the study.

A recording method of -1, 0 or +1 was used with ‘+1’ representing that the definition component was mentioned/ the behavioural aspect was seen and ‘0’ representing the disregard for the component. ‘-1’ was used to denote an active opposition/ contradiction to the behavioural component. This created the data set used for the first analysis.

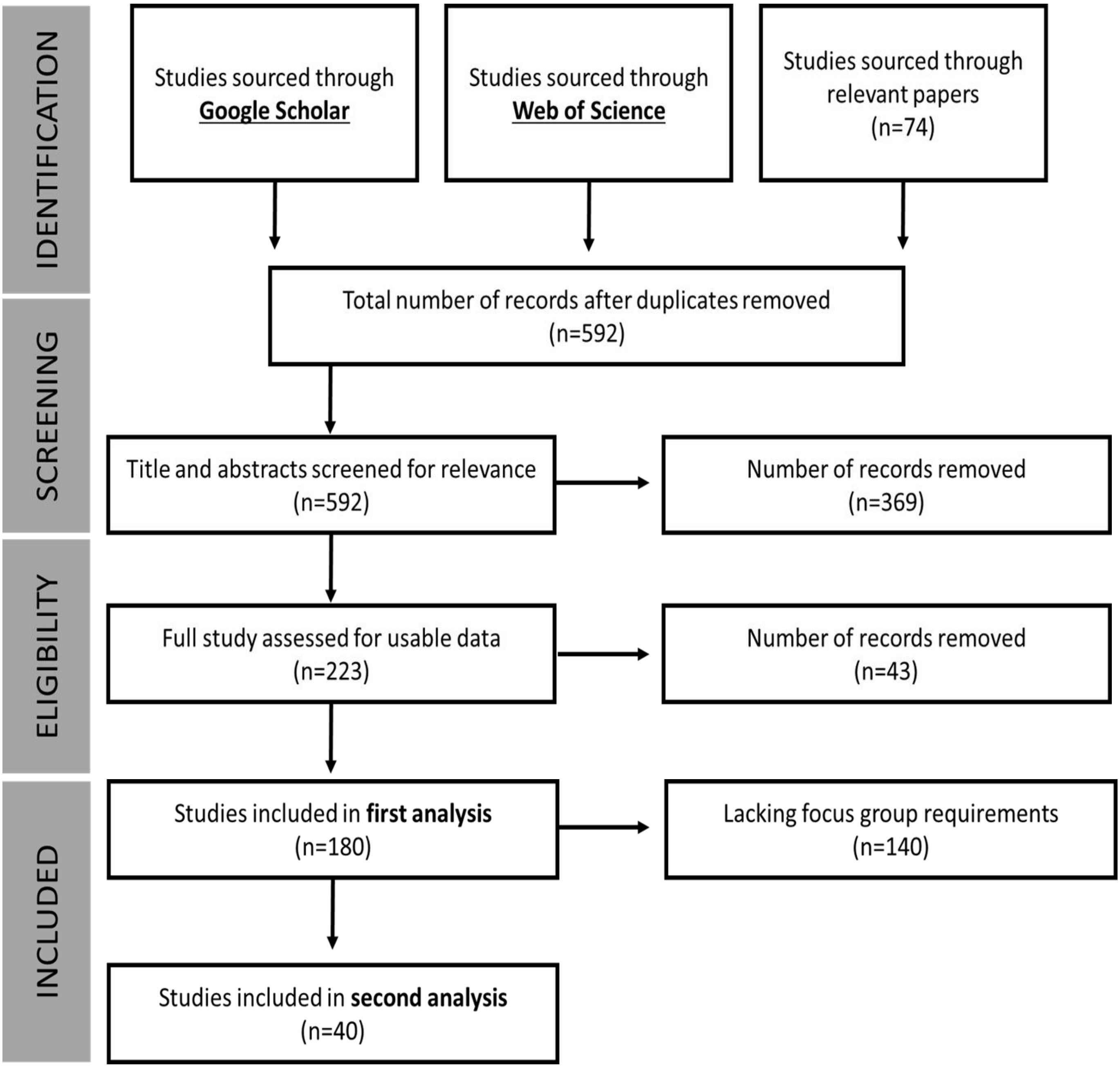


Figure 2: Flow chart outlining the criteria for the inclusion of studies in the systematic literature review following the PRISMA (Preferred Reporting Items for Systematic Reviews) framework.

3.1.3. Second Analysis Dataset

Due to the large variety of taxa and methodologies used to observe behaviour, a secondary dataset was created from the initial dataset to further assess the differences between two targeted categories (primates: polyspecific associations and birds: mixed-species associations). The targeted categories were chosen based on the trends found within the analysis of the first dataset and the descriptive statistics.

Stricter conditions were set for the second analysis to ensure the studies were comparable (Figure 3). First, only studies that researched exclusively birds or primates were shortlisted. Any captive studies were excluded as well as any studies that had purposely manipulated variables thus only wild, observational studies were included. Additionally, any review papers or papers without primary data were also omitted. To study the differences in behaviours between studies using different definitions, study titles must have included ‘polyspecific association’ for primates and ‘mixed species flock/association’ for birds. The dataset followed the same breakdown as the first dataset (Figure 2).

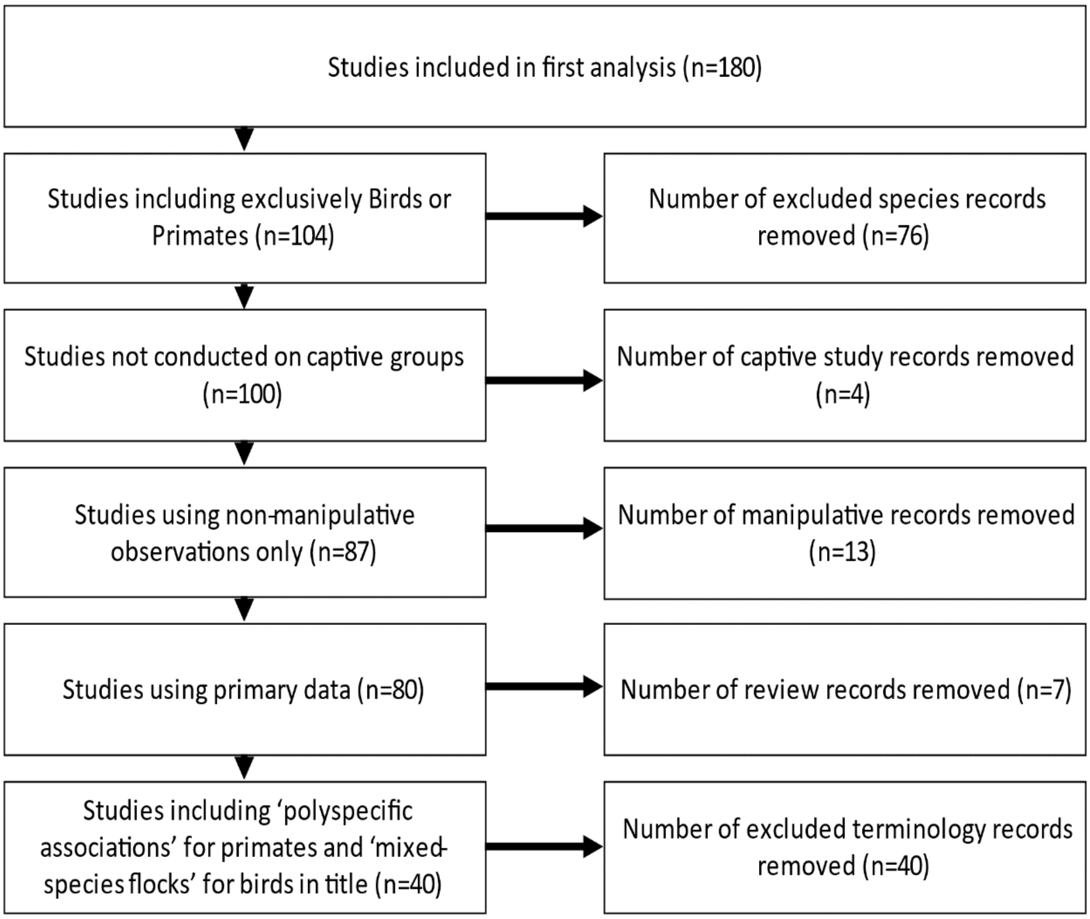


Figure 3: Flow chart outlining the criteria for the inclusion of studies in the secondary refined dataset.

3.1.4. General Variables

All data and information were taken directly from the text, graphs or tables of the studies (Table 4). *Region* and *location* were based on the main site of data collection. Central American locations were categorised with North America. Duplicate studies were catalogued under the initial source. Any study that manipulated conditions or were held in artificial environments were categorised as '*manipulative*'. All literature reviews, meta-analysis or studies using other studies' data were categorised under '*review*'. *Habitat* was assigned into the category of best fit based on the descriptions provided within the individual study. Any studies with multiple locations or lacking data were categorised as '*not-applicable'* within *region*. Similarly, studies with multiple taxa were grouped into '*Inter-order'* and '*not-*

applicable' if they lacked data. Initially, relevant studies were included if key terminology was found in the title or abstract but only studies referencing target terminology (Polyspecific associations in primate studies and Mixed-species flocks/associations in bird studies) in the title were used for the focussed, secondary analysis.

Table 4: Summary and description of initial general variables extracted from studies.

Variables	**Description and range**
ID number	Unique for each study
Reference	Full reference with link if possible
Study sourced from	Google Scholar, Web of Science, ID number of study it was found in
Bibliography pillaged	Yes/no depending on whether the bibliography was used for study sourcing
Publication year	1961-2021
Author(s)	e.g. Waser
Title	e.g. Polyspecific Associations in Primates
Data	Yes/no
Data type	Observational, manipulative, review
Location	Exact location as written in study e.g. Tai National Park, Ivory Coast
Region	Africa, Asia, Australia, Captive, Europe, Marine, NA, North America, South America
Habitat	Urban, Savannah, Agriculture, Temperate Forest, Tropical Forest, Woodland, Marine, Mountain, Cave, Captive, NA
Taxa group	Birds, Inter-order, Mammals, Marine Mammals and Fish, not applicable, Primates, Reptiles and Amphibians
Species 1, 2, 3…	e.g. *Pan troglodytes*, chimpanzee
Terminology	Association, Polyspecific Association, Interspecific Association, Heterospecific Association, Mixed species Association

3.1.5. Definition and Behavioural Variables

The variable *definition* and those for behavioural components were converted into categorical responses to prepare for quantitative analysis (Table 5). Due to the ambiguity of the definitions, many components are not mentioned in all studies - hence the need for an extra response (0 = not mentioned). The initial variable '*different species*' is the only unanimous variable so acted as a quality control to ensure all studies were looking at the correct behaviour. *Chance* was often measured using Waser's Gas Model (1982) however all justified attempts at proving the interaction happened beyond the rate of random occurrence were acknowledged (as '1') within the variable. *Duration* and *Proximity* vary greatly depending on taxa making it difficult to formulate universal parameters. Therefore, the original researcher's discretion was followed for each study to assess whether these variables were within a range worth noting for the species. Any positives that were mentioned for either species as an outcome of the association were recorded under benefits ('1'). Often, researchers commented on the inequality of benefits between the interacting species. This was categorised under '*unequal benefits*'. The frequency of occurrence of this behaviour is divided into '*common/widespread'* or '*rare*'. The studies were grouped into the most fitting category if the universal frequency was discussed. If a species was noted as being key to the association it was considered a '*nuclear species*' regardless of whether 'nuclear' terminology was used. Any inter-order associations directly oppose ('-1') the theory that core species will be similar. Any mention of vagueness, confusion or ambiguity surrounding the behaviour or its definition was recorded in the '*lack of understanding*' variable.

Temporal/ Seasonal changes included daily and annual fluctuations as well as noted changes during lifetime stages (e.g. juvenile) or events (e.g. child-rearing). *Coordinated activities* declared in the study were recorded although many social behaviours, for example grooming, are not present among all taxa so were disregarded from cross-taxa analyses. Behaviour was classified as an interaction if an individual was documented directing a behaviour, action, or vocal cue towards an individual from the other species. This aims to account for the diverse array of social behaviours found across such a large range of taxa. There were two primary drivers described for this behaviour. These were categorised as '*antipredatory benefits'* and '*foraging efficiency'*. Less common drivers such as parasite avoidance and social learning were grouped together in '*other*'.

Table 5: Summary and description of Definition and Behavioural variables extracted from studies.

Categorical variables (1, 0, -1)	**Description**
Different species	Are individuals from 2 or more species interacting?
Chance	Are different species associating more than expected by chance?
Alarm response	Are different species responding to each other's behavioural/ vocal cues intended for intraspecific communication?
Duration	Is the interaction sustained for a prolonged duration?
Proximity	Are individuals of different species within close proximity to one another?
Benefits	Are there benefits that occur from this behaviour?
Unequal benefits	Does the researcher mention the possibility of not all species equally benefiting from this association?
Attraction	Does the researcher note an attraction between the species?
Complexity	Is the behaviour described as complex?
Common/widespread	Has the behaviour been described as common/widespread among life?
Rare	Has the rarity/scarcity of the behaviour been mentioned?
Nuclear species	Is there a key, central species that appears vital to the association? (often described as the 'nuclear species')
Similar core species	Are the main associating species closely related taxa?
Lack of understanding	Is ambiguity/confusion mentioned regarding the definition or the behaviour?
Seasonal /temporal changes	Was there fluctuation in the frequency of the observed behaviour?
Forage/eat	Were species observed foraging or eating together?
Sleep	Were species observed sleeping together?
Travel	Were species observed travelling together?
Defend	Were species observed defending territory together?
Play	Were species observed playing together?
Mating	Were species observed displaying mating behaviour to each other?
Agonistic	Were species observed displaying agonistic behaviour to each other?
Groom	Were species observed grooming each other?
Rest	Were species observed resting together?

Categorical variables (1, 0, -1)	Description
Interactions	Were any overall interactions between species observed?
Antipredatory benefits	Did the researcher mention antipredatory advantages to the species as a cause for the association?
Foraging efficiency	Did the researcher mention foraging efficiency for the species as a cause for the association?
Other	Did the researcher mention other advantages to the species as a cause for the association?

1 = yes, 0 = not mentioned, -1 = no.

3.2. Statistical Analysis

3.2.1. Descriptive Statistics

The initial analysis uses the first dataset to summarise and provide visual representation of the data. Different groups of variables (Taxa, Region, Habitat) were compared in their association with the four target terminologies (polyspecific, mixed-species, heterospecific, interspecific association) to show the general trends in terminology use within behavioural ecology. Association category was added to represent all titles that included the term. Associations such as ‘foraging association’ and ‘hunting association’ that are excluded from the other categories are represented here. Studies that include multiple terms in their title are represented in both categories, thus sum of datapoints does not equal sum of studies used.

3.2.2. Multiple Correspondence Analysis (MCA)

Each variable used in the MCA was assigned a unique categorical code (e.g. Proximity = P1, P0, P-1). The selected definition segments were run through MCA using the FactoMineR (Le et al. 2008) and ggplot2 (Wickham 2016) packages in R (R Core Team 2020). MCA was used as it analyses datasets with categorical data (Abdi and Valentin 2007).

3.2.3. Principal Component Analysis (PCA)

A principal component analysis highlights patterns within multivariate data by converting the inter-correlated quantitative variables into a set of uncorrelated variables to show similarity within the data (Abdi and Williams 2010). The recorded variables that correspond to aspects of the definition were identified. A PCA was run using FactoMineR (Le et al. 2008) and ggplot2 (Wickham 2016) packages in R (R Core Team 2020).

3.2.4. Cluster Analysis

Cluster analysis gathers data into the most mathematically similar groups based on the multivariate data (Romesburg 2004). A cluster dendrogram was produced in R (R Core Team 2020) to visually represent the relationships between the data and to confirm discrepancies between datasets. A further discriminant function analysis was run to observe the studies' probability of being classified in their respective taxonomic clades based on the defining criteria and behavioural categories.

4. Results

4.1. Trends of Data – Descriptive Statistics

The associative behaviour this paper is focussed on has been known by many different names. Specific terminology popularity varies greatly throughout the dataset. Graphical representations of the collective studies depict the fluctuation of terminology usage taxonomically, geographically, ecologically, and temporally.

4.1.1. Terminology Breadth across Taxa

Despite the terminology 'polyspecific associations' being around for decades it is, for the most part, exclusively favoured by primatologists to describe multi-species associations demonstrating the inconsistency of terminology used throughout the animal kingdom for these similar behaviours (Figure 4). The term 'polyspecific associations' is used comparatively negligibly other than in primatology which points to this terminology describing a unique association that is only evident in restricted taxa. Mixed species associations seem to be less specific and potentially a more encompassing definition as it is used in a range of taxa and the spread is far more consistent, being favoured by bird, mammal, marine and general studies.

Studies were included in the association category if they included the word 'association' in the title regardless of its preface so incorporated terms such as "hunting" and "foraging" association. These associations are often more generalised because they rarely occur beyond their specific defined purposes, and they are seldom describing fully integrated groups of two or more species as witnessed in some other studies.

Figure 4 shows relatively high use of the term 'association' among inter-order studies; however, it scores low in the remaining categories. The conclusion can therefore be drawn that the inter-order associations are less profound than the associations among more closely related species.

The terms heterospecific and interspecific are less common and are evenly spread among all taxa. Due to the lack of usage within the studies it raises questions about the need for so many different defining terms.

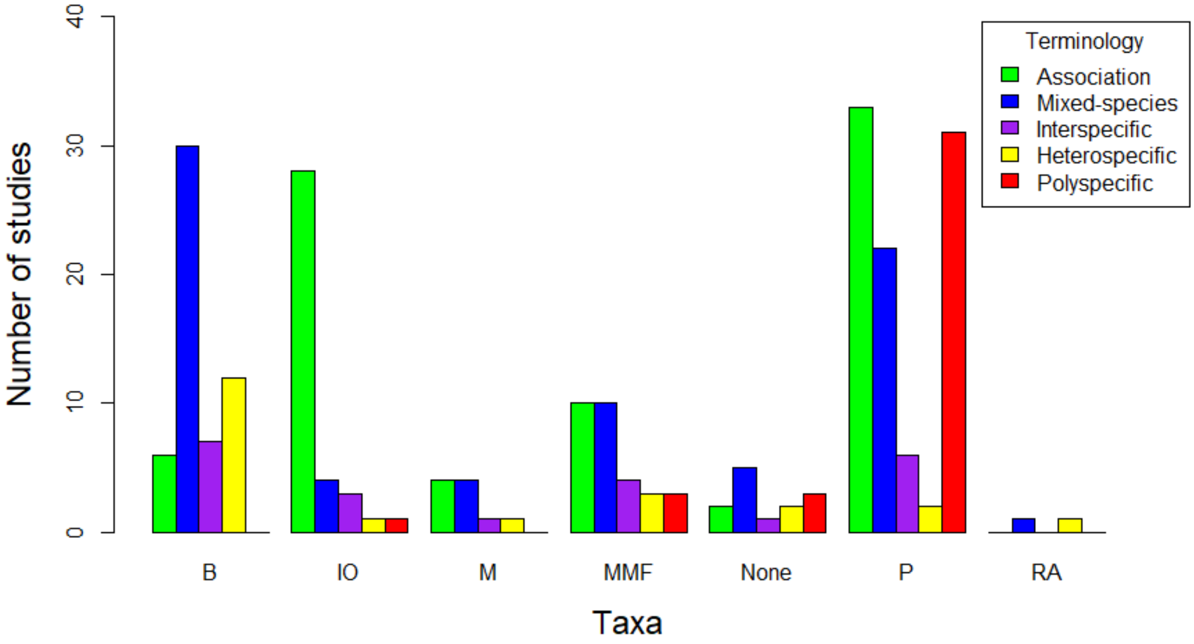


Figure 4: Breadth of terminology used across papers on different taxa. B = Birds, IO = Inter-order, M = Mammals**, MMF = Marine Mammals and Fish, None = not applicable***, P = Primates, RA = Reptiles and Amphibians. *Study observed association between 2 species from different categories. **mammals not included in other categories. ***no focus species/ overview paper.*

4.1.2. Terminology Breadth across Region

The breadth across regions of multi-species associative terminology is relatively uniform (Figure 5). Polyspecific associations is only used in tropical regions which coincides with the spread of diversity across the globe as the vast majority of primates are found exclusively in these continents and general biodiversity is also higher. We can also see a preference for the term heterospecific in Asia in comparison to other geographical regions. Europe, Australia and captive have a low volume of studies within the dataset so it is difficult to form a representative conclusion about their terminology usage. It is interesting to note that all of these regions have no mention of interspecific or polyspecific associations.

The reason for disparity within terminology across the globe could be the result of cultural investigator bias, i.e. different regions are exposed to a different range of vocabulary and therefore names of behaviours are sometimes adapted and evolved. The most likely cause of the fluctuation in terminology across regions is the overall biodiversity trends across the world. With tropical countries having significantly higher diversity than temperate, it is also the most likely place for complex and novel associative behaviours to emerge.

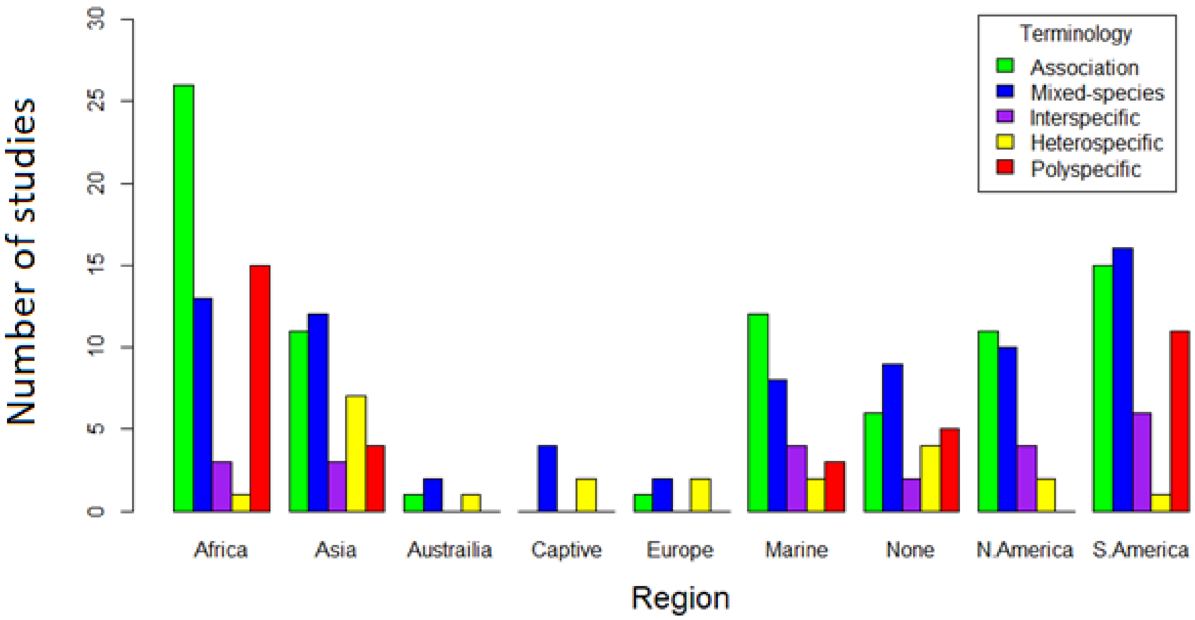


Figure 5: Breadth of terminology use in literature based on region they were studied in. None = no focus species/ overview paper. N. America = North America. S. America = South America. Central American studies categorised within North America (N. America).

4.1.3. Terminology Breadth across Habitat

The habitat preference for species displaying this associating behaviour is predominantly forest (Figure 6). This is likely due to the numerous bird and primate occurrences within the dataset. Discounting the absence of interspecific terminology within artificial environments, the terminology is proportionally very evenly spread across the data. There are no distinct or unusual discrepancies when looking at the percentage spread, other than the aforementioned, indicating that habitat has little/no impact on the choice of terminology used among researchers.

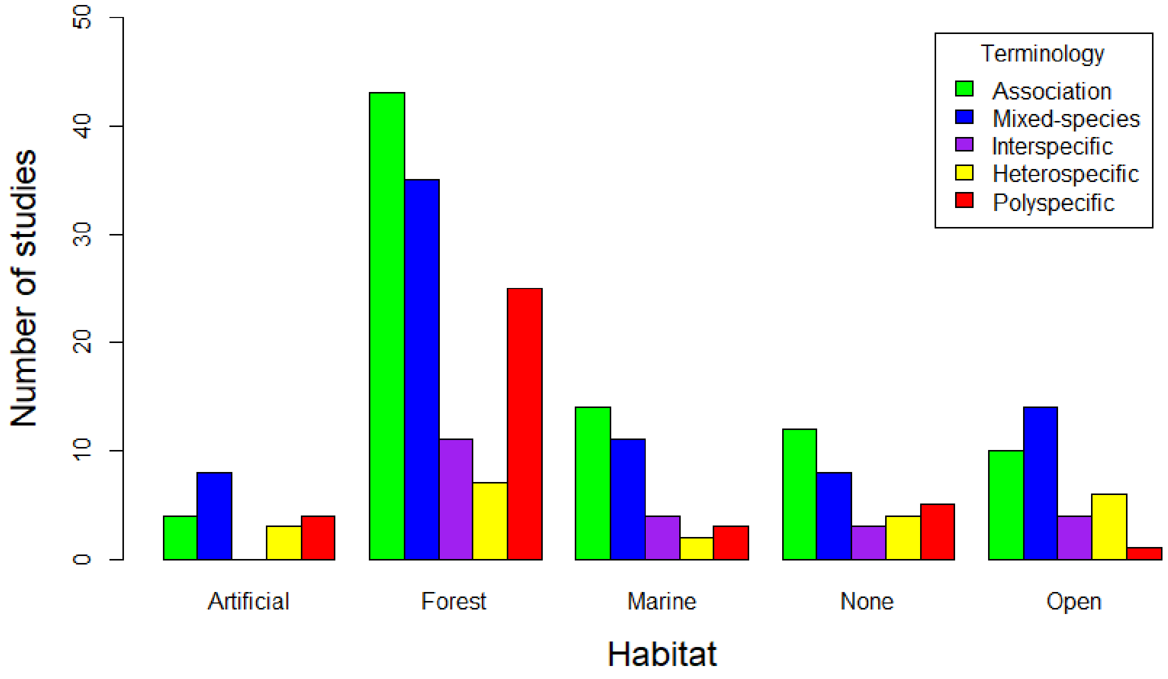


Figure 6: Breadth of terminology use in literature based on habitat they were studied in. None = no focus habitat, habitat unclear or overview paper. Artificial includes agricultural land, captivity and urban environments. Open includes grassland, savannah, montane and shrubland environments.

4.2. Analysis of Defining Criteria

The inconsistencies within the use of terminology among researchers is apparent across many variables especially taxonomically. To begin to ascertain the nature of these discrepancies, we must extract the defining criteria used within the studies and analyse the underlying differences. This will help to create a clearer picture on whether the behaviours are distinct or overlapping in criterion and thus whether separate terminology or dissolution into one encompassing terminology would provide the clearest foundation for what researchers can use to describe this behaviour.

4.2.1. Multiple Correspondence Analysis – All Taxa

The initial multiple correspondence analysis (MCA) analyses definition components across all studies to discover any similarities and assess any overall trends in definitions used between taxa. The first two dimensions depicted in (Figure 7) explain relatively little (31.8%; Table 6) of the variance between studies and the model needs 8 dimensions to explain the recommended 80% of cumulative percentage variance. This means the studies either had potentially observed different behaviours or used different diagnostic criteria.

Using the scree plot (Figure 8) we can see the biggest drop of percentage variance explained appears after the first dimension indicating the variables that contribute most to dimension 1 may have important roles in distinguishing the differences in the data between taxa.

By using the squared correlations between variables and the dimensions as coordinates, we can visualise and identify the most correlated variable with each dimension (Figure 9). It can be seen that ‘chance’ (i.e. whether authors mentioned the importance of whether meetings were more frequent than expected by chance) and ‘duration’ (i.e. whether authors reported a minimum duration of the behaviour) are most heavily correlated with the first dimension and have little effect on dimension 2. On the other hand, differences in the nuclear species variable (i.e. mention of one species being nuclear to the behaviour) or whether the species are taxonomically similar are likely to be seen on the dimension 2 axis.

The central point ‘DS1’ in the main MCA plot negates its effect equally on both dimensions due to all studies describing behaviour between 2 disparate species. Dimension 1 appears to segregate (using the y-axis) whether the variable was present and mentioned (‘variable+1’) or whether the variable was not mentioned/ ignored by the paper (‘variable+0’). This is also where the main visual trend lies between taxa – the red primate nodes favouring the left side with the present variables and the blue bird nodes favouring the right. The only positive variable that has bird nodes closer than primate nodes is the presence of a nuclear species (N1). This is also the only positive node that is slightly on the right side of the horizontal axis where the majority of bird nodes lie. The same nodes are simultaneously pooled around MC-1 meaning these studies are likely to have found that the occurrence of the observed association may have happened by chance. Many inter-order data points were located close to SS-1 as the phylogenetic distance between the species involved in the association acted as direct opposition to the claim that this behaviour only happens between species that are taxonomically similar. Other taxa showed no trends and thus diluted the percentage explanation of variance. Therefore, a further analysis was warranted to look solely at the disparities between bird associations and primate associations.

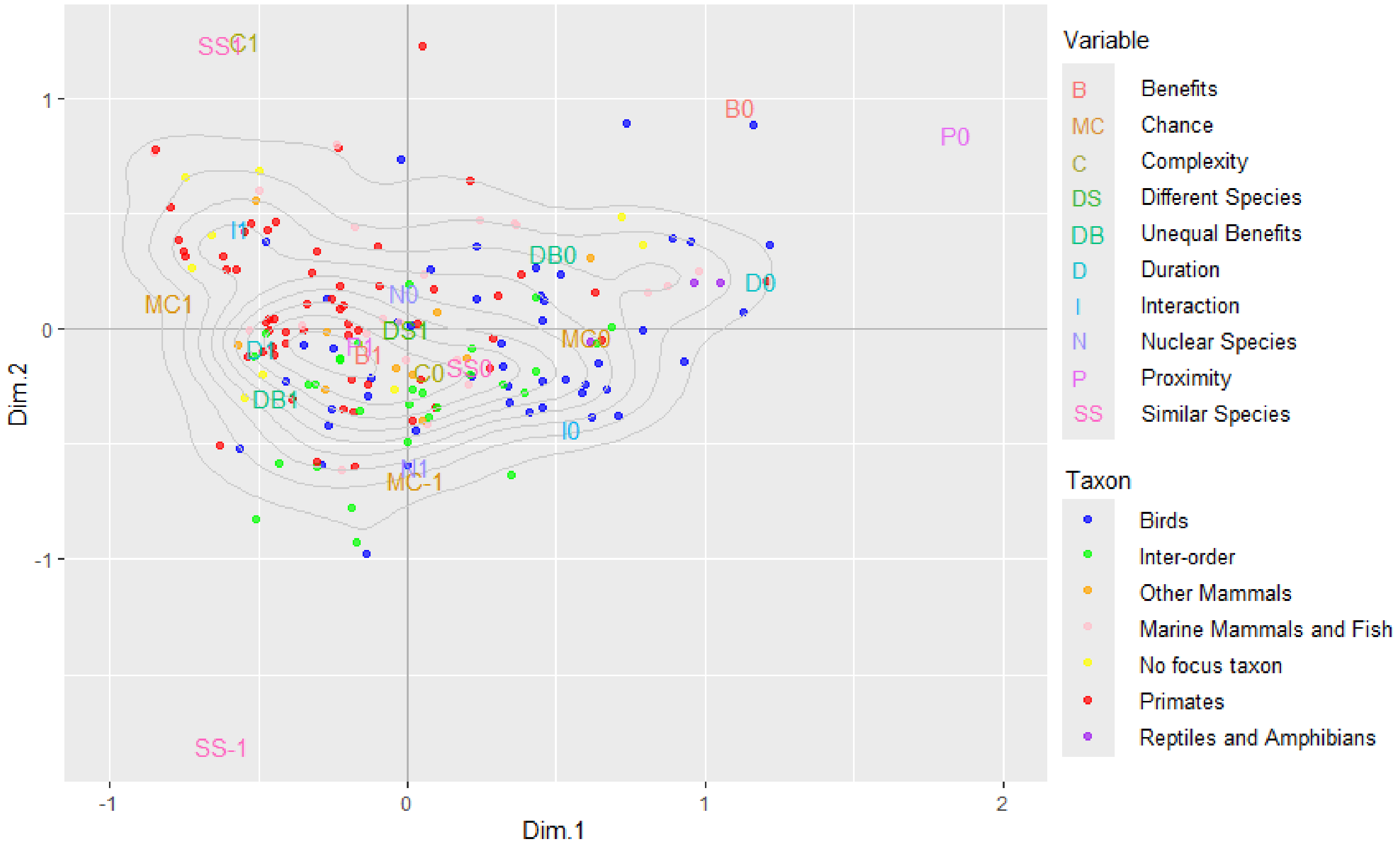


Figure 7: Relationship between taxa and the common definition segments found in associative behaviour studies from the initial dataset. Shown by a multiple correspondence analysis. Jittered (0.1).

Table 6: Eigen value and percentage variance for all studies in the initial dataset using multiple correspondence analysis.

Dimension	**Eigen value**	**Percentage of variance**	**Cumulative percentage of variance**
1	0.216	19.658	19.658
2	0.134	12.143	31.801
3	0.127	11.581	43.382
4	0.113	10.312	53.694
5	0.098	8.934	62.628
6	0.091	8.243	70.871
7	0.079	7.179	78.049
8	0.071	6.458	84.507
9	0.062	5.675	90.182

10	0.059	5.331	95.513
11	0.049	4.487	100.000

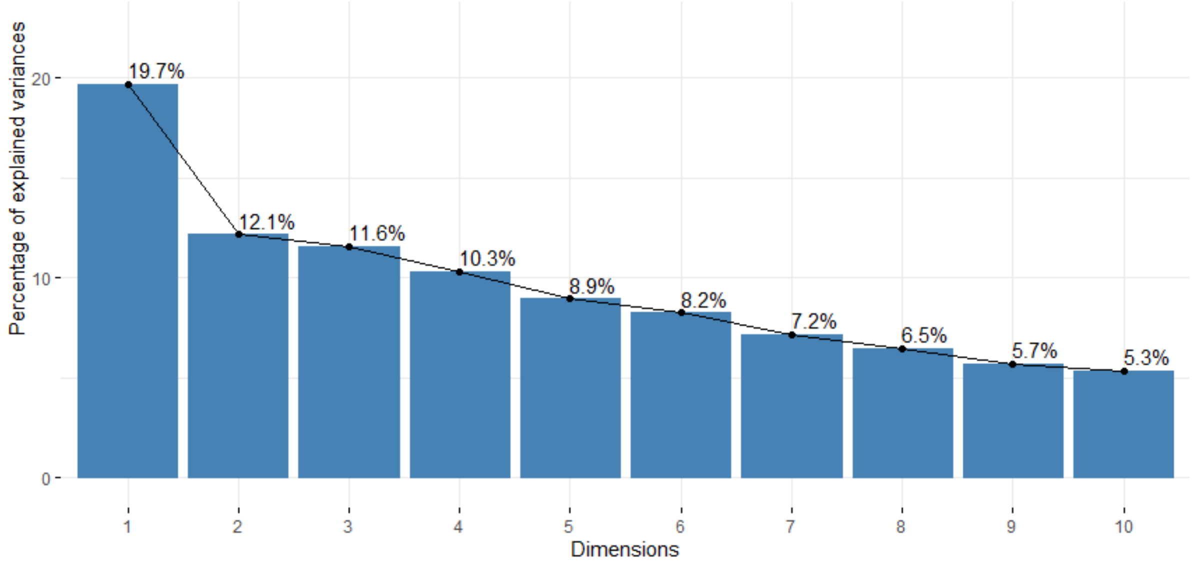
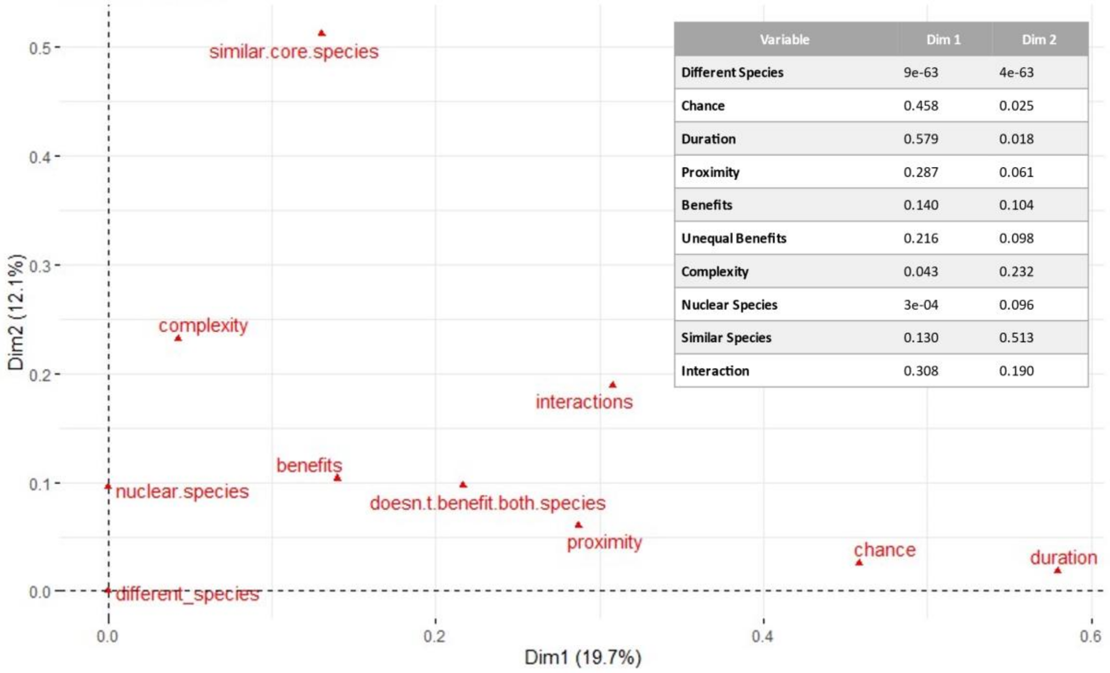


Figure 8: Scree plot showing the percentage of explained variances for each dimension in the multiple correspondence analysis of the initial dataset.



Variable	Dim 1	Dim 2
Different Species	9e-63	4e-63
Chance	0.458	0.025
Duration	0.579	0.018
Proximity	0.287	0.061
Benefits	0.140	0.104
Unequal Benefits	0.216	0.098
Complexity	0.043	0.232
Nuclear Species	3e-04	0.096
Similar Species	0.130	0.513
Interaction	0.308	0.190

Figure 9: Correlation between variables and principal dimensions for the initial dataset in multiple correspondence analysis.

4.2.2. Principal Component Analysis – Reduced Taxa Categories

Reducing the taxon categories to 'primates', 'birds' and 'other' offers a clearer picture of the main trend across the whole dataset (Figure 10). There is a higher explanation of variance across all dimensions (Table 7). 43.8% of explained variance can be visualised graphically within the first 2 dimensions of the PCA and over a quarter of all variance can be explained in the first dimension (Figure 11). Birds and primates seem to gravitate towards opposite ends in the main PCA plot despite a fairly even spread of all other taxa. This solitary trend aligns with the spread of terminology across data points found in the previous descriptive statistics (Figure 4).

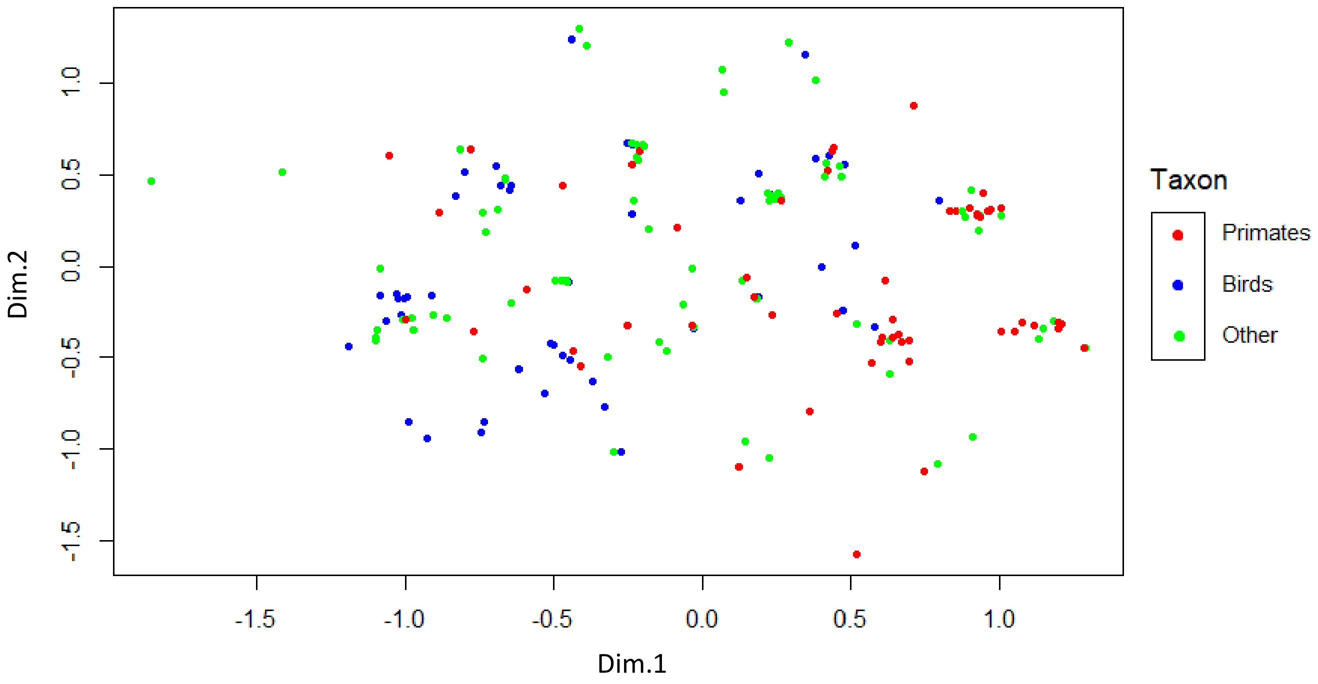


Figure 10: Principal component analysis separation of the initial dataset showing how the focus taxa (primates and birds) are correlated with the definition variables. Jittered (0.1). Other = all remaining taxa groups that do not include birds or primates.

Table 7: Eigen value and percentage variance for all studies in the initial dataset using principal component analysis.

Dimension	Eigen value	Percentage of variance	Cumulative Percentage of variance
1	0.485	27.257	27.257
2	0.292	16.520	43.777
3	0.224	12.667	56.445
4	0.187	10.563	67.008
5	0.178	10.082	77.089
6	0.151	8.504	85.593
7	0.097	5.487	91.080
8	0.078	4.415	95.495
9	0.057	3.242	98.736
10	0.022	1.264	100.000

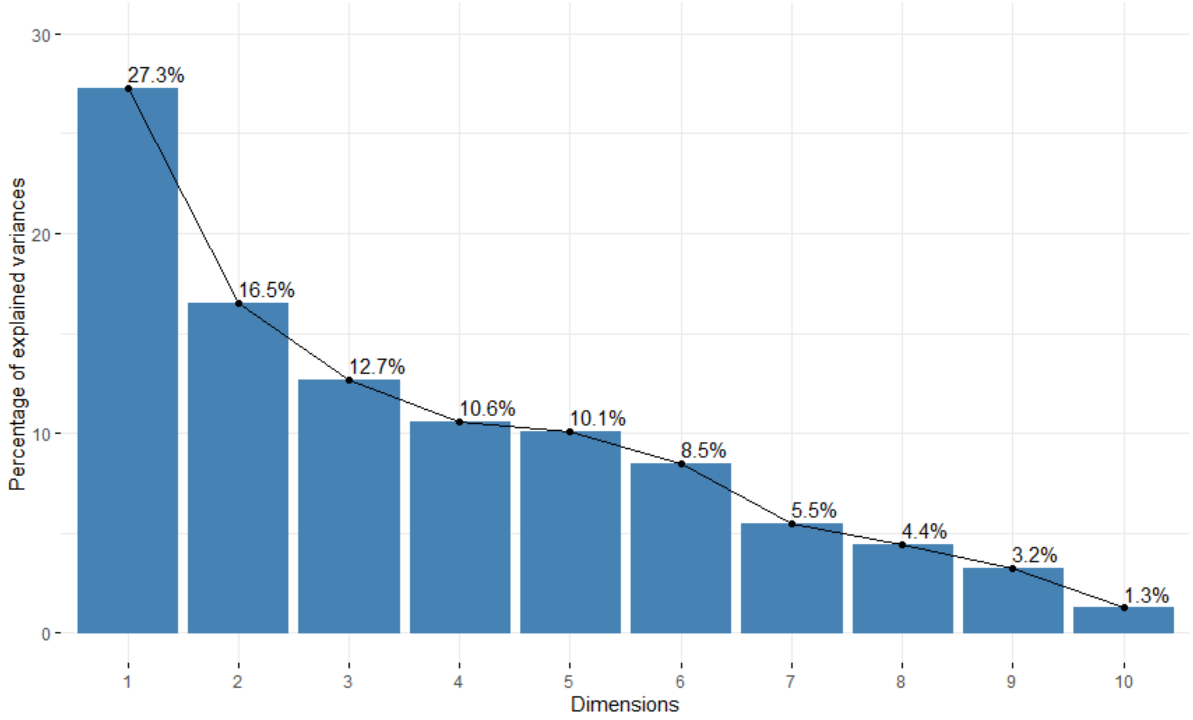


Figure 11: Scree plot showing the percentage of explained variances for each dimension in the principal component analysis of the initial dataset.

4.2.3. Principal Component Analysis – Terminology

Figure 12 displays the spread of data in relation to the terminology used in the study. Polyspecific associations have the most notable trend favouring the right. This follows a similar pattern to the spread of taxon in Figures 7 and 10 as well as the descriptive statistics. This highlights the need to focus on a reduced dataset that not only analyses the differences between bird and primate studies but also the uniqueness of 'Polyspecific Associations'.

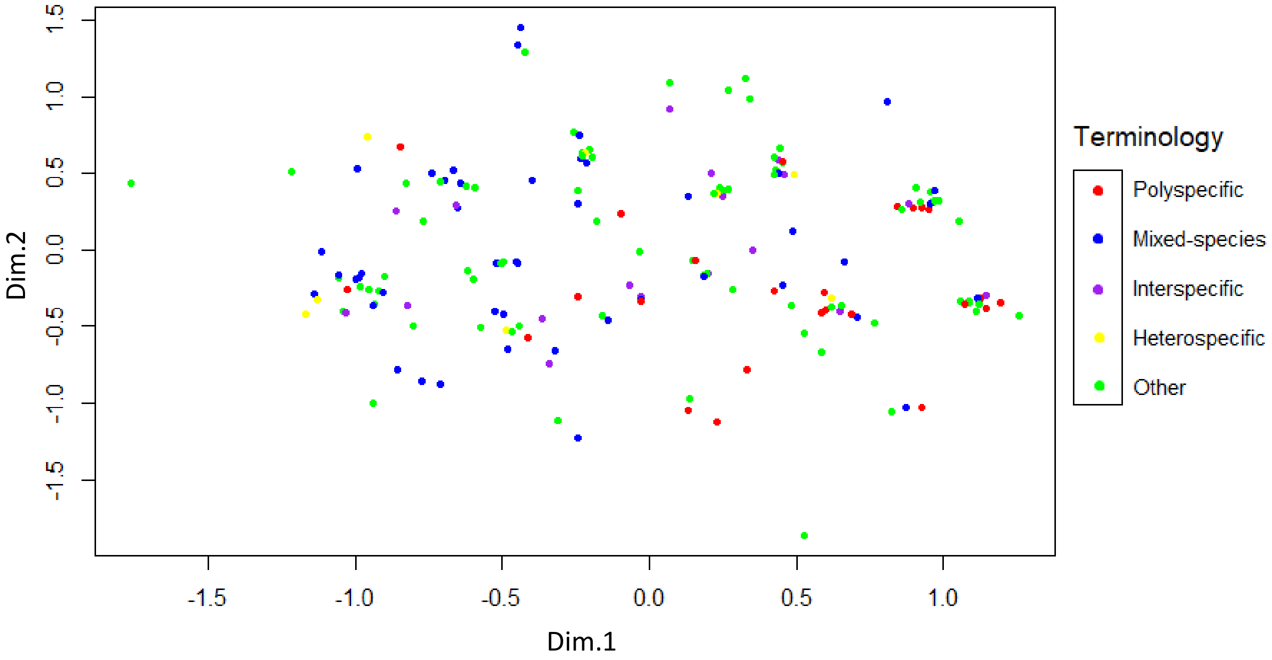


Figure 12: Principal component analysis separation of the initial dataset showing how the main terminologies are correlated with the definition variables. Jittered (0.1).

4.2.4. Multiple Correspondence Analysis – Reduced Dataset 'Primates:PSA' and 'Birds:MSA'

By using a reduced dataset that exclusively includes 'Primates:PSA' and 'Birds:MSA' we start to see a higher explanation of variance in a multiple component analysis (Table 8). The first dimension explains over a quarter (25.2%) of the variance and the visual variance explanation (dimension 1 + dimension 2) reaches 42% (Figure 14). There is also a clearer divide between the 2 data groups in the main MCA plot (Figure 13). The primate nodes pool around the majority of positive '1' variables and the bird nodes pool around the unmentioned variables. This points to a lack of thorough standardised research methods, particularly in bird mixed species flock studies. There are some exceptions to the aforementioned trend such as the variables that are connected with benefits. Bird studies may have more discussion on the benefits of the association and the inequality of benefits among individuals/species due to the blue node pooling around 'B1' and 'DB1'. Similarly, the acknowledgement of a 'nuclear species' (N1) is exclusively clustered by blue nodes and on the opposing side from the rest of the positive variables suggesting a key characteristic when defining mixed species associations among birds.

The most correlated variables to dimension one now includes proximity in combination with chance and duration (Figure 15). Complexity is also correlated to almost solely dimension one but to a far lesser extent. 'Interaction', 'benefits', and 'different species' variables seem to have fairly equal and negligible impact on these dimensions. This means these variables are encompassing defining criteria and should be discounted when distinguishing definition differences between polyspecific associations in primates and mixed species flocks in birds. The remaining variables that are mainly clustered by blue nodes are more correlated with dimension 2.

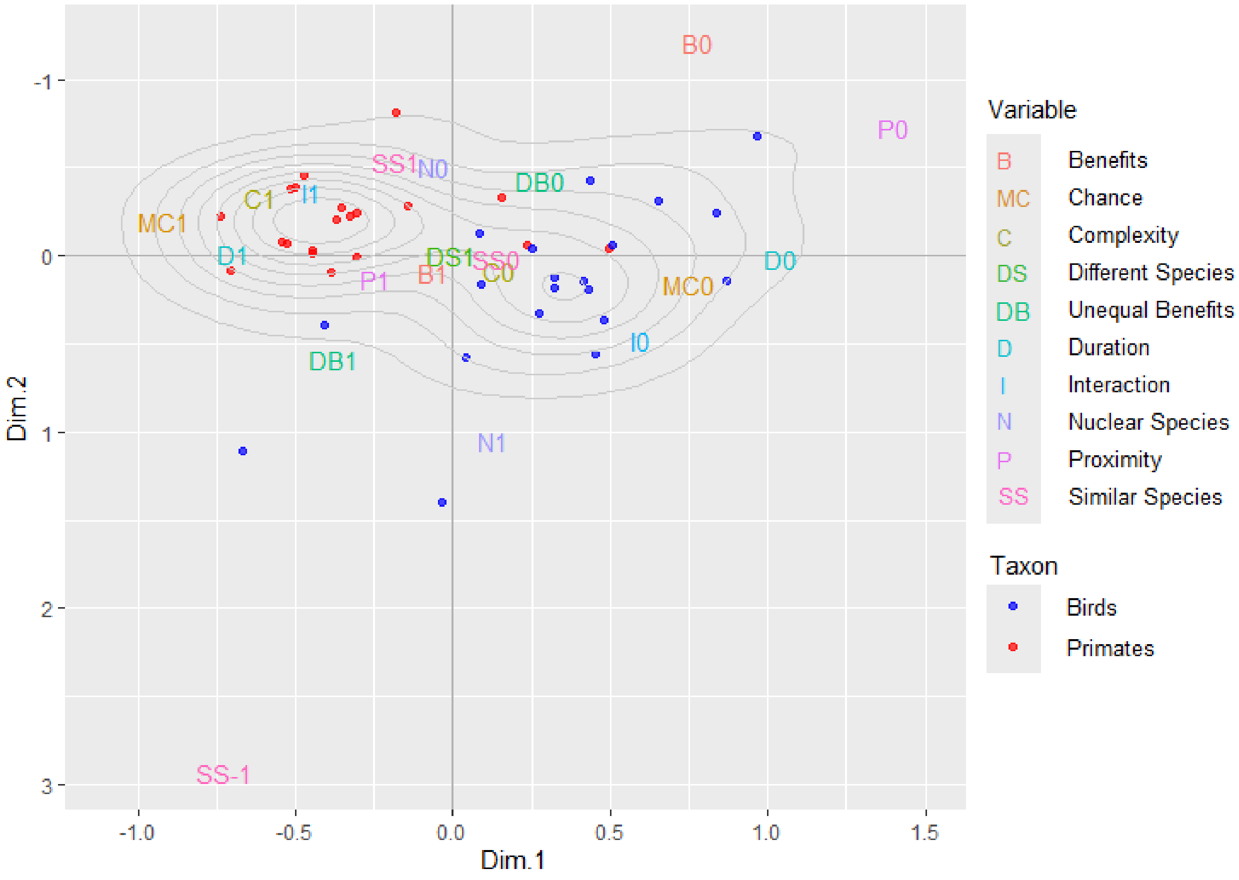


Figure 13: Relationship between the focus taxa (birds and primates) and the common definition segments found in associative behaviour studies from the refined dataset. Shown by a multiple correspondence analysis. Jittered (0.1).

Table 8: Eigen value and percentage variance for reduced dataset ('primates: polyspecific associations' and 'birds: mixed-species associations') using multiple correspondence analysis.

Dimension	**Eigen value**	**Percentage of variance**	**Cumulative Percentage of variance**
1	0.252	25.239	25.239
2	0.168	16.844	42.083
3	0.122	12.157	54.240
4	0.103	10.257	64.497
5	0.090	9.001	73.498
6	0.071	7.137	80.635
7	0.064	6.420	87.056
8	0.057	5.695	92.751
9	0.046	4.619	97.370
10	0.026	2.630	100.000

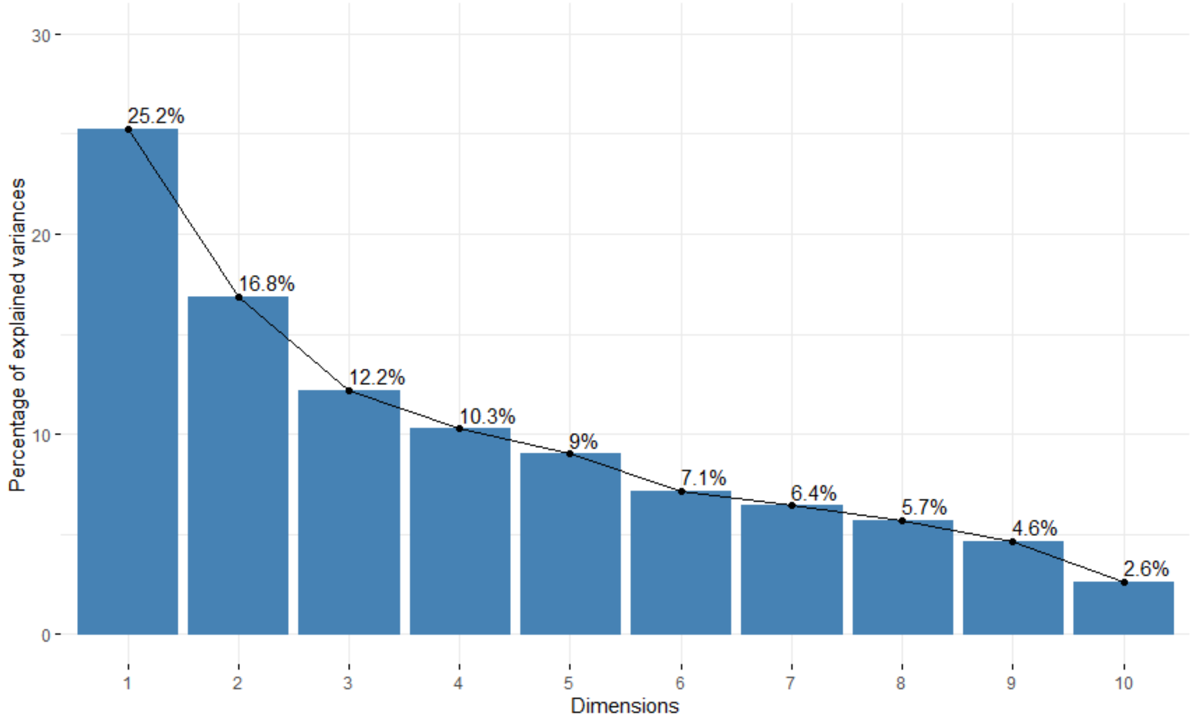
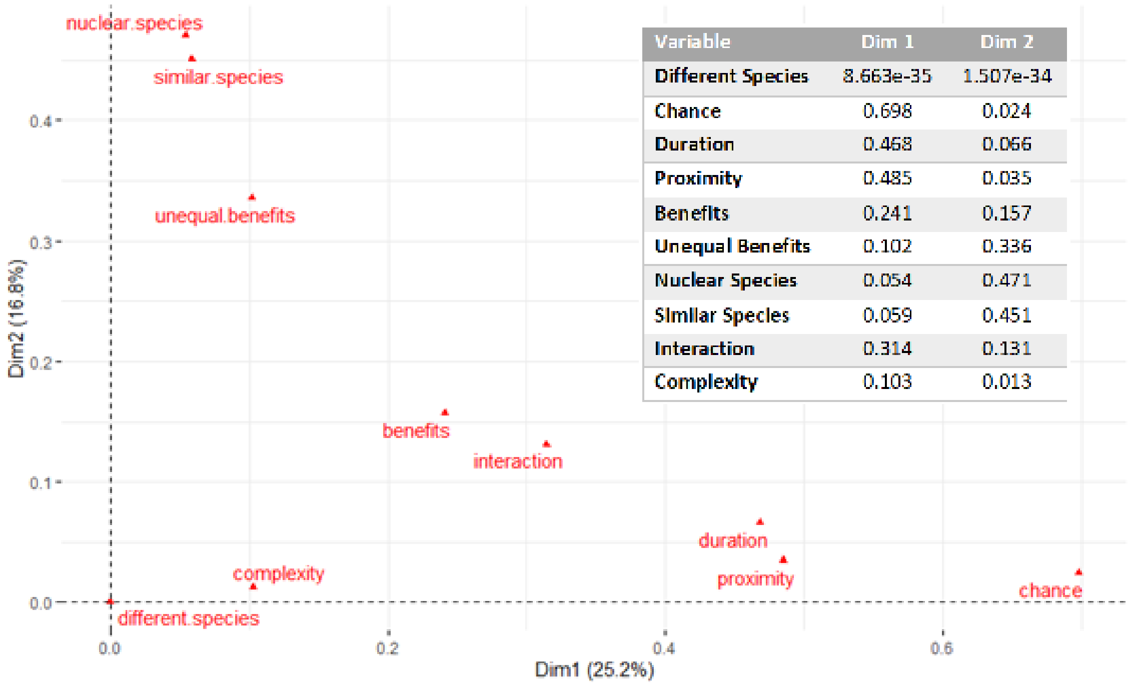


Figure 14: Scree plot showing the percentage of explained variances for each dimension in the multiple correspondence analysis of the reduced dataset ('primates: polyspecific associations' and 'birds: mixed-species associations').



Variable	Dim 1	Dim 2
Different Species	8.663e-35	1.507e-34
Chance	0.698	0.024
Duration	0.468	0.066
Proximity	0.485	0.035
Benefits	0.241	0.157
Unequal Benefits	0.102	0.336
Nuclear Species	0.054	0.471
Similar Species	0.059	0.451
Interaction	0.314	0.131
Complexity	0.103	0.013

Figure 15: Correlation between variables and principal dimensions for reduced dataset ('primates: polyspecific associations' and 'birds: mixed-species associations') in multiple correspondence analysis.

4.2.5. Principal Component Analysis – Reduced Dataset 'Primates:PSA' and 'Birds:MSA'

The arrows on the PCA (Figure 16; Figure 17) using the reduced dataset cluster around the horizontal and point towards the side primarily frequented with primates thus reaffirming the definition fragments are more applicable in Primates:PSA as opposed to Birds:MSA studies. The longest arrows and hence the most influential defining criteria for primates are whether the study acknowledged the need for the association to be beyond chance encounters (MC), whether sustained duration was upheld (D), and whether the researcher felt the association needed to exist exclusively between biologically similar species (SS). Two arrows that fall away from the majority point towards the Birds:MSA studies which implies Bird:MSA studies are more likely to include nuclear species (N) and inequality of benefits (DB) in their research. Benefits and complexity have very small arrows indicating that they are insignificant when trying to ascertain the key differences between the 2 groups of data. Similarly, the variable representing the behaviour requiring more than one species is central as this is true for all studies in the dataset. The explanation of variance in the visible 2 dimensions almost reaches 50% using this analysis (47.9%) - the highest witnessed from this dataset (Table 9). The large drop between the initial 2 dimensions and the rest of the dimensions are witnessed using a scree plot (Figure 18). The drop indicates the high likelihood that the key variance between the data can be visualised on the main plot and the main variables that contribute to dimensions one and two are the defining differences between Primates:PSA and Birds:MSA. The corr plot (Figure 19) visualises the strength that each variable is correlated with each dimension. The strongest correlations and thus the most likely to be influencing the divide are chance, duration and interaction variables in dimension 1 and unequal benefits and similar core species in dimension 2.

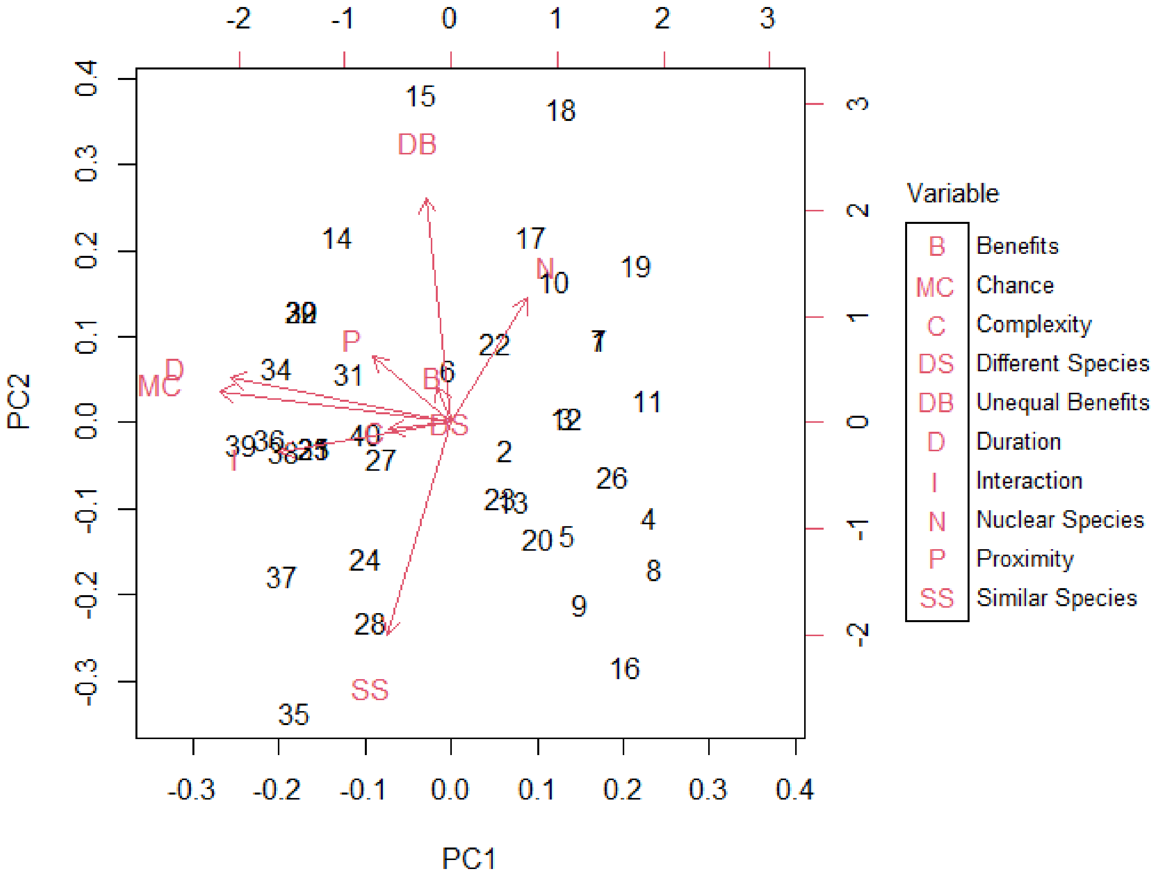


Figure 16: Numbered biplot of principal component analysis separation of 'primates: polyspecific associations' and 'birds: mixed-species associations'. Birds:MSA studies = 1-20. Primates:PSA studies = 21-40.

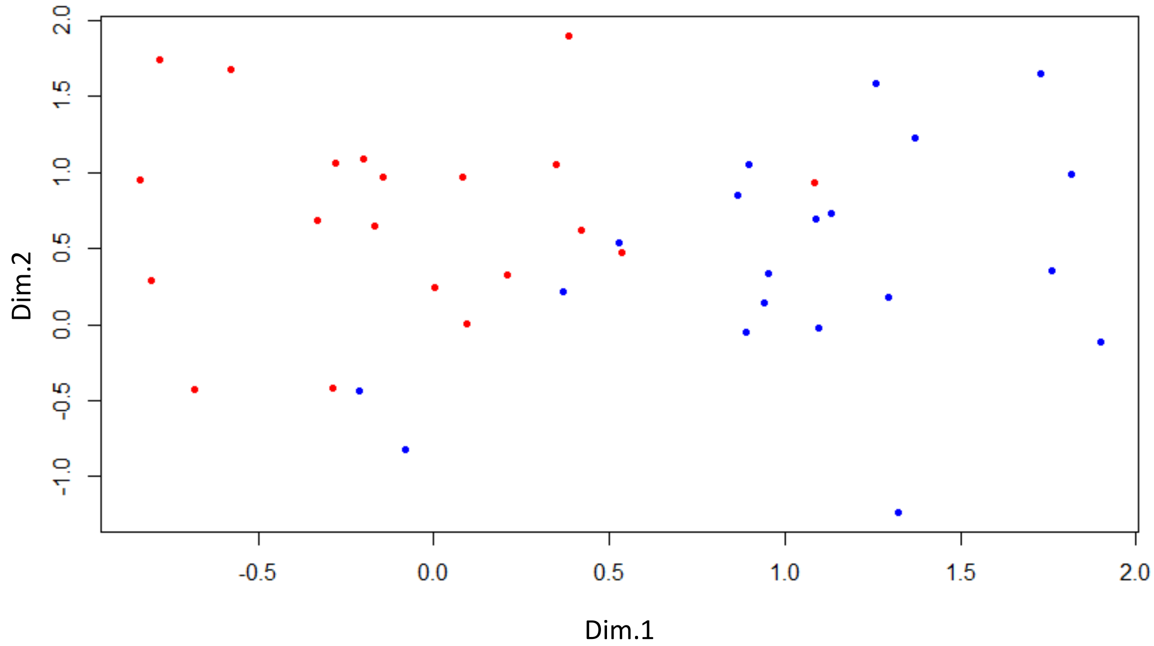


Figure 17: Principal component analysis separation of 'primates: polyspecific associations' and 'birds: mixed-species associations' Showing how the focus groups are correlated with the definition variables. Blue = Birds:MSA, red = Primates:PSA.

Table 9: Eigen value and percentage variance for reduced dataset ('primates: polyspecific associations' and 'birds: mixed-species associations') using principal component analysis.

Dimension	**Eigen value**	**Percentage of variance**	**Cumulative Percentage of variance**
1	0.531	26.800	26.800
2	0.417	21.055	47.855
3	0.220	11.116	58.971
4	0.202	10.203	69.174
5	0.190	9.591	78.765
6	0.152	7.681	86.446
7	0.103	5.216	91.662
8	0.083	4.172	95.833
9	0.058	2.945	98.778
10	0.024	1.222	100.000

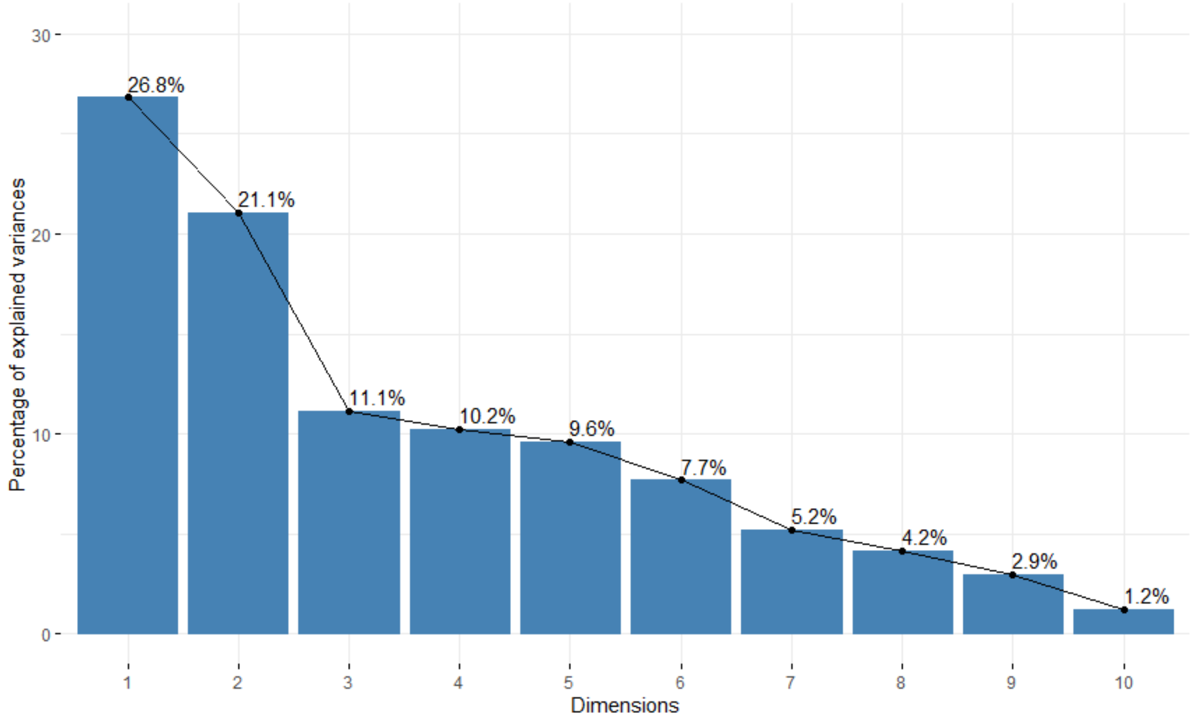


Figure 18: Scree plot showing the percentage of explained variances for each dimension in the principal component analysis of the reduced dataset ('primates: polyspecific associations' and 'birds: mixed-species associations').

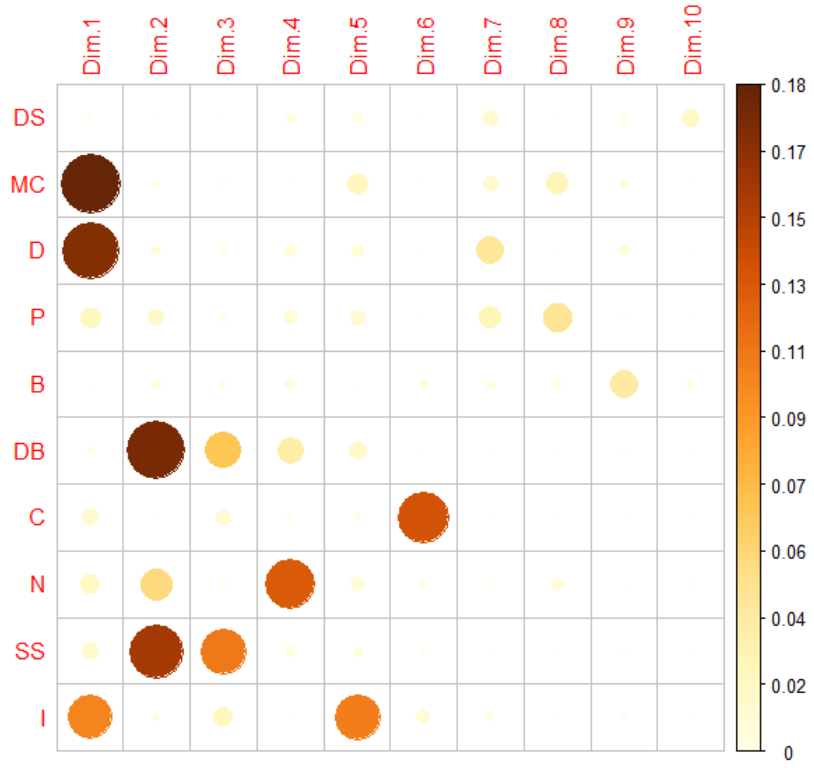


Figure 19: Contribution of variables to each dimension variances for reduced dataset ('primates: polyspecific associations' and 'birds: mixed-species associations') using principal component analysis.

4.2.6. Cluster Dendrogram – Reduced Dataset 'Primates:PSA' and 'Birds:MSA'

The Cluster Dendrogram (Figure 20) further provides evidence of the fundamental differences between Primates:PSA and Birds:MSA studies. The second division splits primates and birds with only 4 outliers (14, 22, 23, 26). An additional discriminant function analysis of this dataset predicted the only true outlier was study 14.

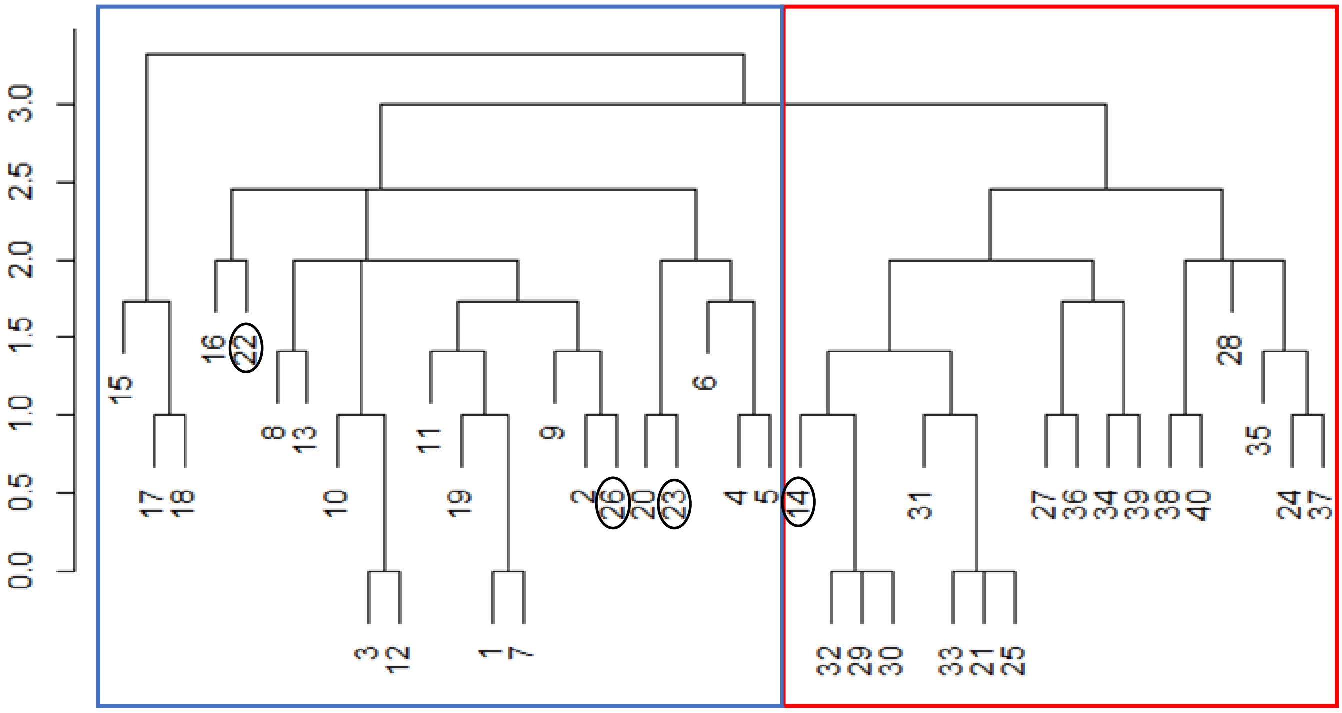


Figure 20: Cluster Dendrogram of 'Primates: polyspecific associations' and 'Birds: mixed-species associations'. Birds:MSA studies = 1-20. Primates:PSA studies = 21-40. Blue = Birds:MSA best predicted split, red = Primates:PSA best predicted split. Circled numbers indicate outliers found in further discriminant function.

4.3. Analysis of Behaviour

By collecting data on the comparable behaviours that are common within single-species groups of both birds and primates, we can analyse if there are patterns within the data. This can help decipher whether the focus associations should be categorised under a single umbrella term or are distinct enough to warrant separate unique terminology.

4.3.1. Multiple Correspondence Analysis – Behaviour

There is a fairly steady decrease in percentage variance visualised in the scree plot (Figure 21). The first two dimensions only explain 35% of variance and it takes 11 dimensions to fully explain the dataset. The amount of behavioural component variables can be held partly accountable for a low explained variance. The primary 3 dimensions explain almost half of the variance (49.942%; Table 10) and the biggest drop comes after dimension 3. This indicates that the behavioural components that dominate these dimensions are the most crucial in distinguishing the key differences between datapoints.

Table 10: Eigen value and percentage variance for behaviour using multiple correspondence analysis.

Dimension	**Eigen value**	**Percentage of variance**	**Cumulative percentage of variance**
1	0.300	19.116	19.116
2	0.255	16.201	35.317
3	0.230	14.625	49.942
4	0.169	10.753	60.695
5	0.155	9.835	70.530
6	0.137	8.741	79.271
7	0.095	6.055	85.326
8	0.083	5.301	90.627
9	0.070	4.456	95.083
10	0.047	2.978	98.061
11	0.030	1.939	100.000

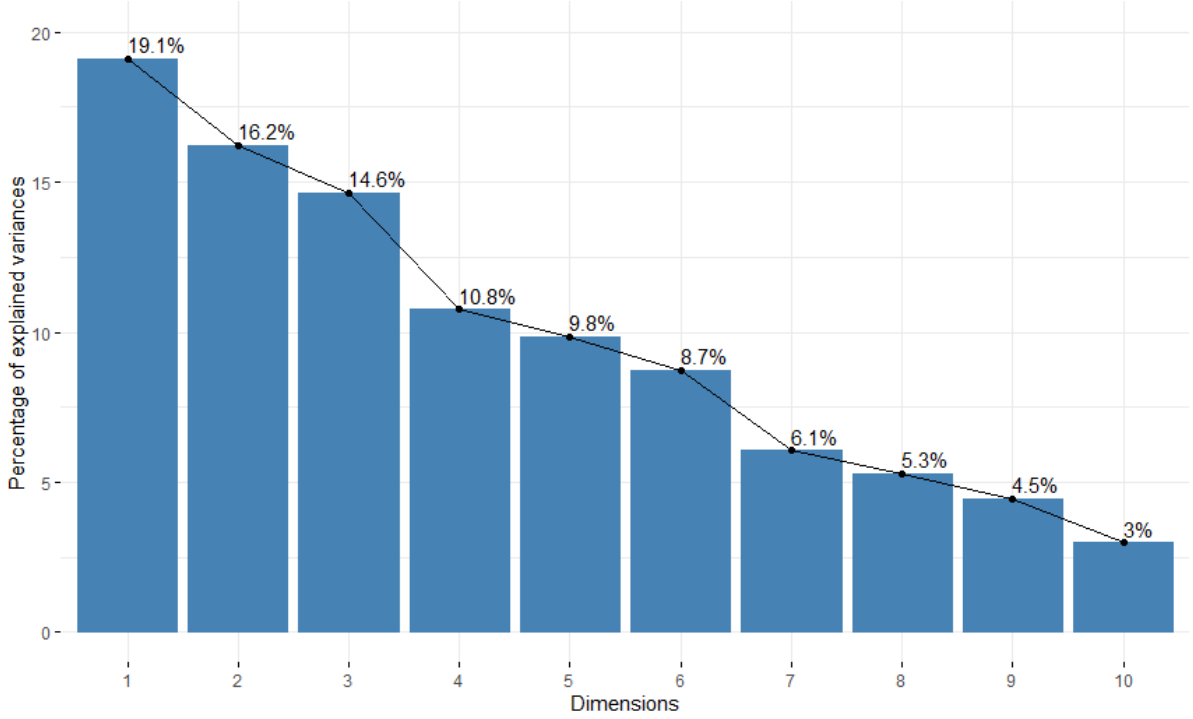


Figure 21: Scree plot showing the percentage of explained variance for each dimension in the multiple component analysis of behavioural component variables in primate and birds.

The MCA plot (Figure 22) shows many anomalies in the dataset, particularly in primates whose observed behaviour contradicts what the other studies found for example 'no coordinated travel' (T-1) and not foraging together (F0). Despite the irregularities there is still an overall segregation between the red and blue nodes that is governed by the primary dimension along the horizontal. It is interesting to note that the blue bird nodes have two distinct 'pools' that seem to be split by the second dimension. The upper blue pool is centred around the absent variables ('0's) suggesting that their studies observed very little behaviour so it is unclear how complex the behavioural interactions are within these associations. The lower blue pool gravitates towards associations where species travel together (T1) and do not display any agonistic behaviour towards the opposing species (A-1) however they do not defend their territory as a collective either (DE-1).

The red primate nodes are once again pooled around most of the positive variables ('1's) this includes resting, foraging and travelling together; responding to each other's alarm calls; and low seasonality/temporal changes. They gravitate towards behavioural components that traditionally oppose many definitions for mixed-species/polyspecific associations such as agonistic behaviour, lack of coordinated travel and high seasonal and temporal changes.

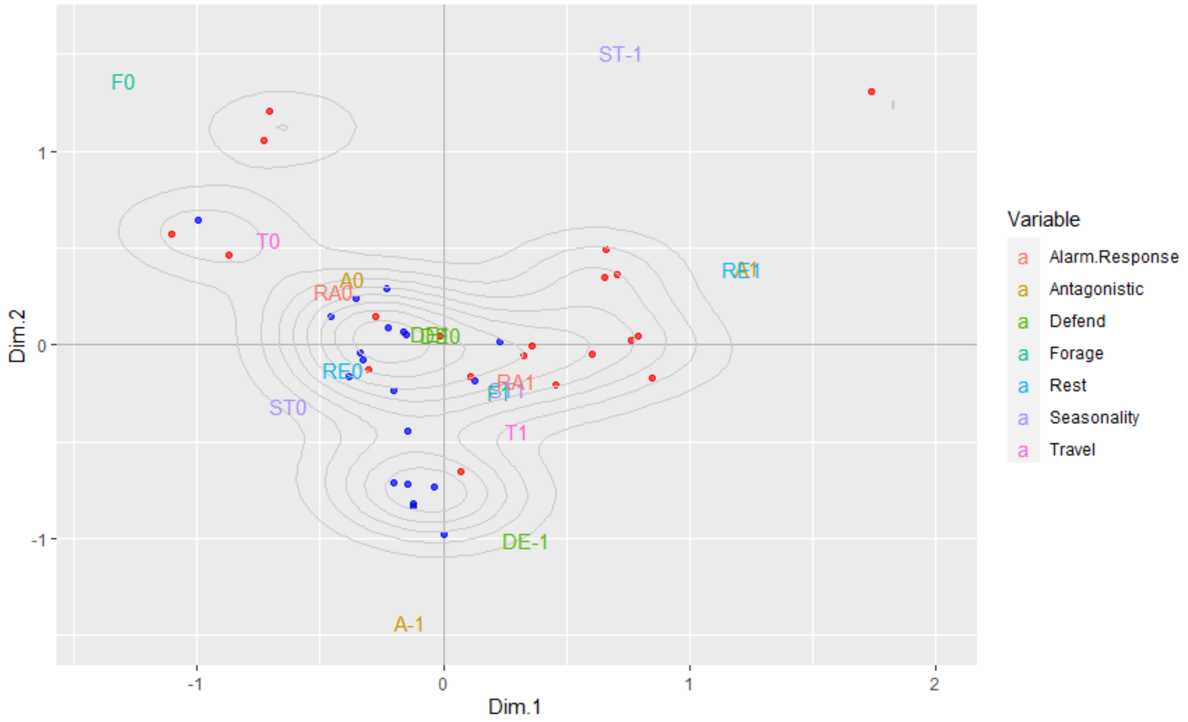


Figure 22: Relationship between taxa and the common behaviours found in associative behaviour studies from the refined dataset. Shown by a multiple correspondence analysis. Blue nodes = 'Birds: mixed-species associations'; Red nodes = 'Primates: polyspecific associations'. Jittered (0.1).

4.3.2. Principal Component Analysis - Behaviour

By using a principal component analysis, we begin to see a far larger proportion of the variance explained. Over a quarter of the variance (27.700%) is explained by the initial dimension and over half (50.431%) within the first 2 dimensions that we are able to visualise using plots (Table 11). There are far fewer dimensions (7) to explain all of the variance than previous analyses which can be seen using the scree plot (Figure 23) and to reach 80% which is the target percentage for most standard PCAs it takes 4 dimensions.

Table 11: Eigen value and percentage variance for behaviour using principal component analysis.

Dimension	**Eigen value**	**Percentage of variance**	**Cumulative percentage of variance**
1	0.562	27.700	27.700
2	0.461	22.731	50.431
3	0.330	16.247	66.678
4	0.265	13.053	79.731
5	0.201	9.925	89.656
6	0.144	7.106	96.762
7	0.066	3.238	100.000

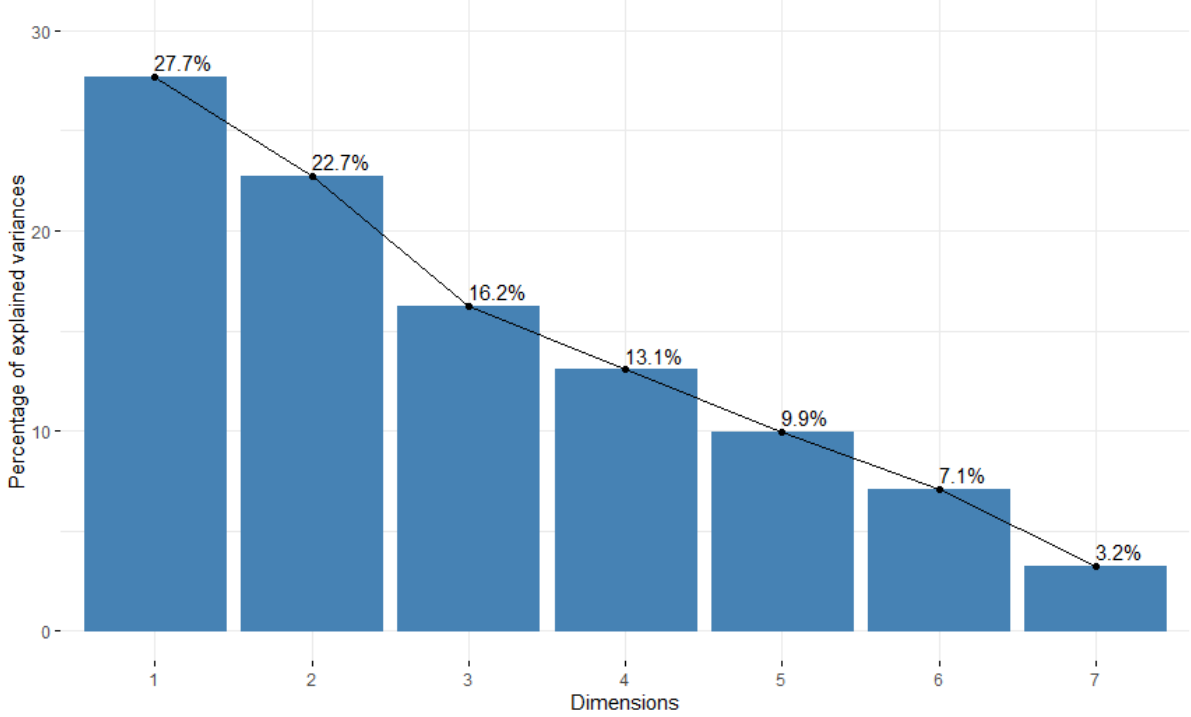


Figure 23: Scree plot showing the percentage of explained variance for each dimension in the principal component analysis of behavioural variables in primate and birds.

All variables seem to act mostly independently from one another, each dominating a single dimension with fairly little impact on the others (Figure 24). There are no behavioural variables that seem to be consistently found together within the studies and the combination of variables from study to study appear random regardless of taxa or terminology used.

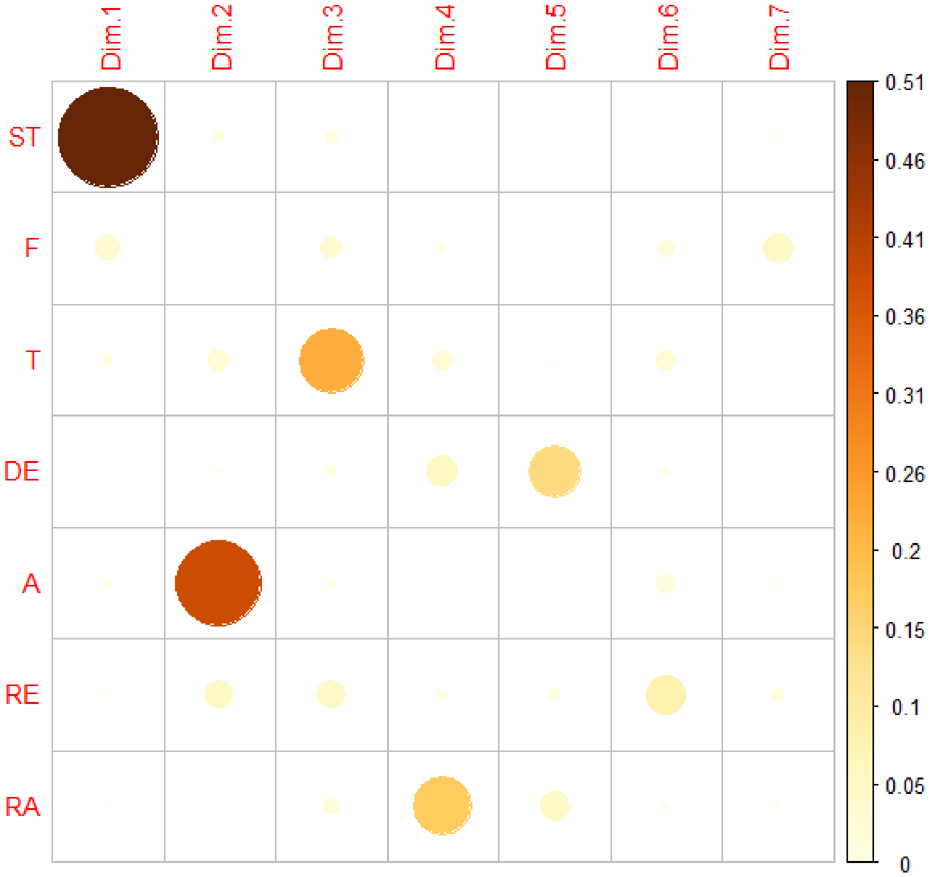


Figure 24: Contribution of variables to each dimension variances for reduced dataset ('Primates: polyspecific associations' and 'Birds: mixed-species associations') using principal component analysis.

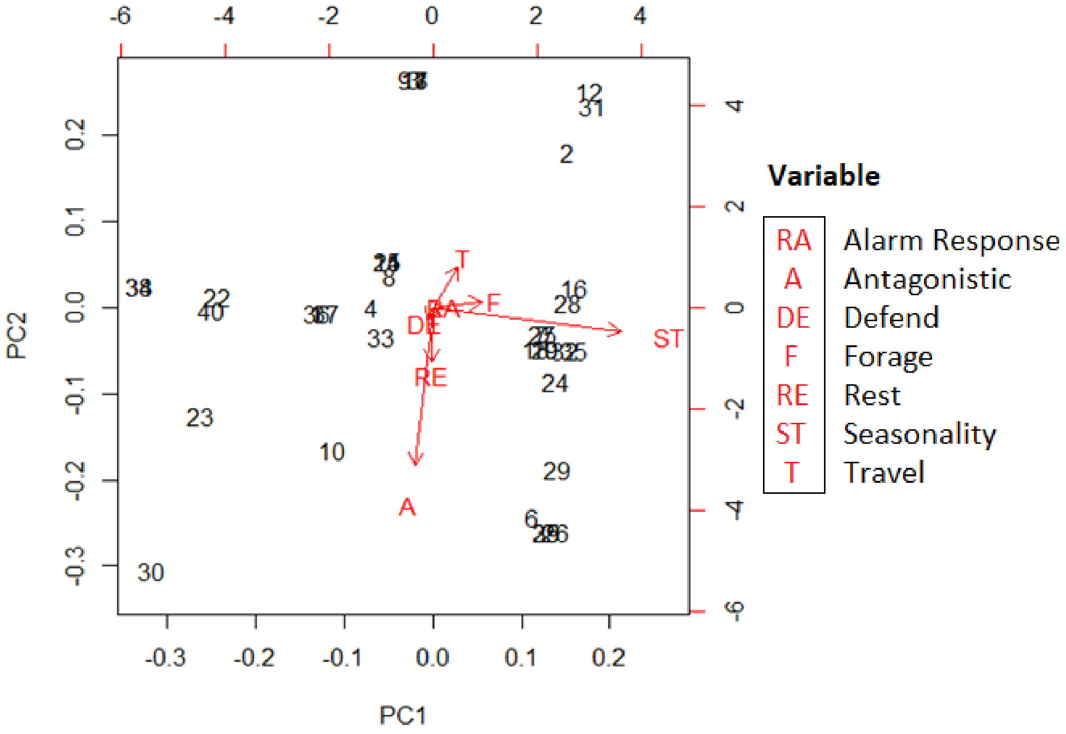
Seasonal and temporal changes in associations (ST) had the biggest impact on the PCA. This variable almost solely contributes to the first dimension and over a quarter of the variance within the dataset. The horizontal divergences within the PCA (Figure 25) can therefore be attributed to the stability and consistency of the association. The negative (left) side of the horizontal is dominated by primates in polyspecific associations studies. Therefore, on average, primate polyspecific associations are more fluid and temporary than birds in mixed species flocks.

The vertical second dimension is primarily influenced by agonistic interactions (A) between individuals from different species. The split is not as clear, however, by focusing on the areas of highest vertical divergence (+/- 0.5) we can see that the lower section which is most likely to have agonistic interactions observed in the study is primarily frequented by primates. A majority of bird studies in the upper quarter of the PCA (Figure 25) indicates that agonistic behaviour is rare and unlikely to be observed within Birds: mixed-species flocks.

Foraging (F) and responding to the other species alarm calls (RA) follow a similar trend to seasonality but have a much smaller influence on the dataset (Figure 25). Therefore primates in polyspecific associations are more likely to forage together and react to alarms made outside of their species group than birds in mixed-species flocks. Similarly, primates from my dataset are more likely to rest together (RE) due to the variable following a trajectory alike to agonistic interaction.

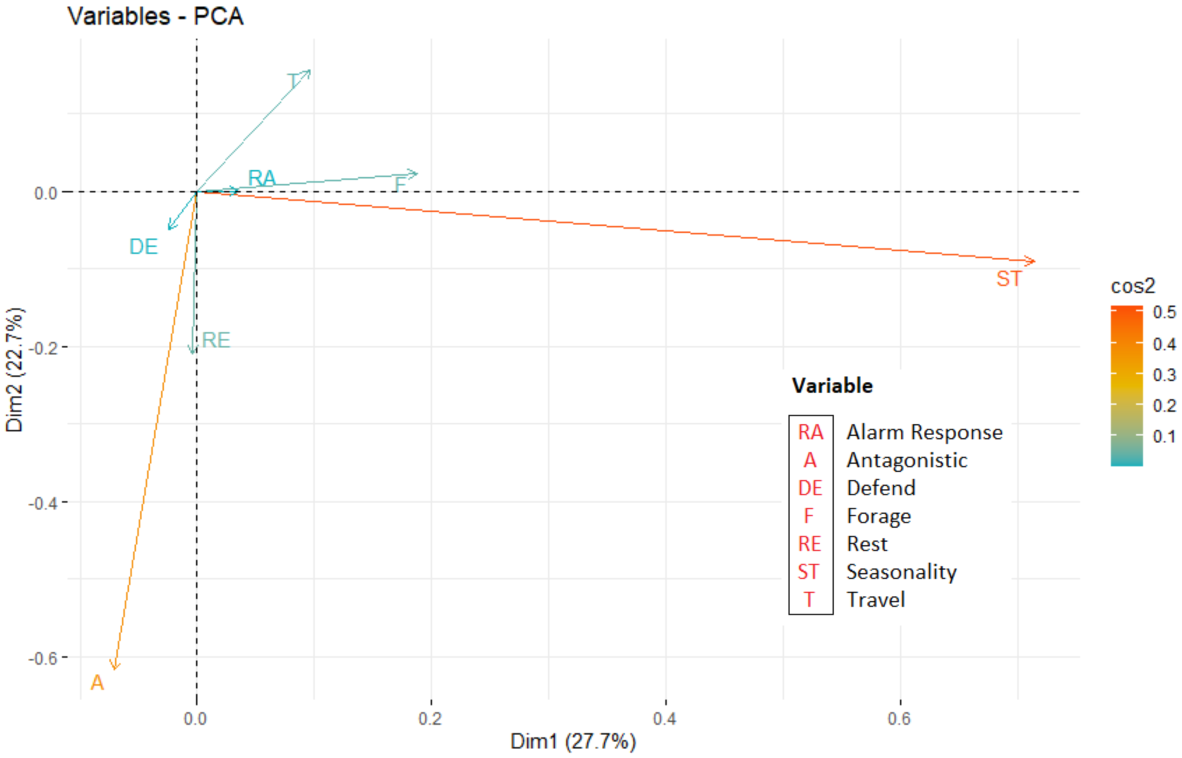
The travel (T) and co-defending territory (DE) variables have diagonal trajectories pointing in opposite directions. The nodes they are pointing to are fairly evenly spread so despite travel being the third largest contributor to the explanation of variance in the data (Figure 24), they cannot be used to distinguish between primates and birds or polyspecific associations and mixed-species associations.

A)



PC1
PC2
-0.3
-0.2
-0.1
0.0
0.1
0.2
-6
-4
-2
0
2
4
RA
A
DE
F
RE
ST
T
Variable
RA Alarm Response
A Antagonistic
DE Defend
F Forage
RE Rest
ST Seasonality
T Travel

B



Variables - PCA
Dim1 (27.7%)
Dim2 (22.7%)
0.0
0.2
0.4
0.6
-0.2
-0.4
-0.6
T
RA
F
DE
RE
ST
A
cos2
0.5
0.4
0.3
0.2
0.1
Variable
RA Alarm Response
A Antagonistic
DE Defend
F Forage
RE Rest
ST Seasonality
T Travel

C.

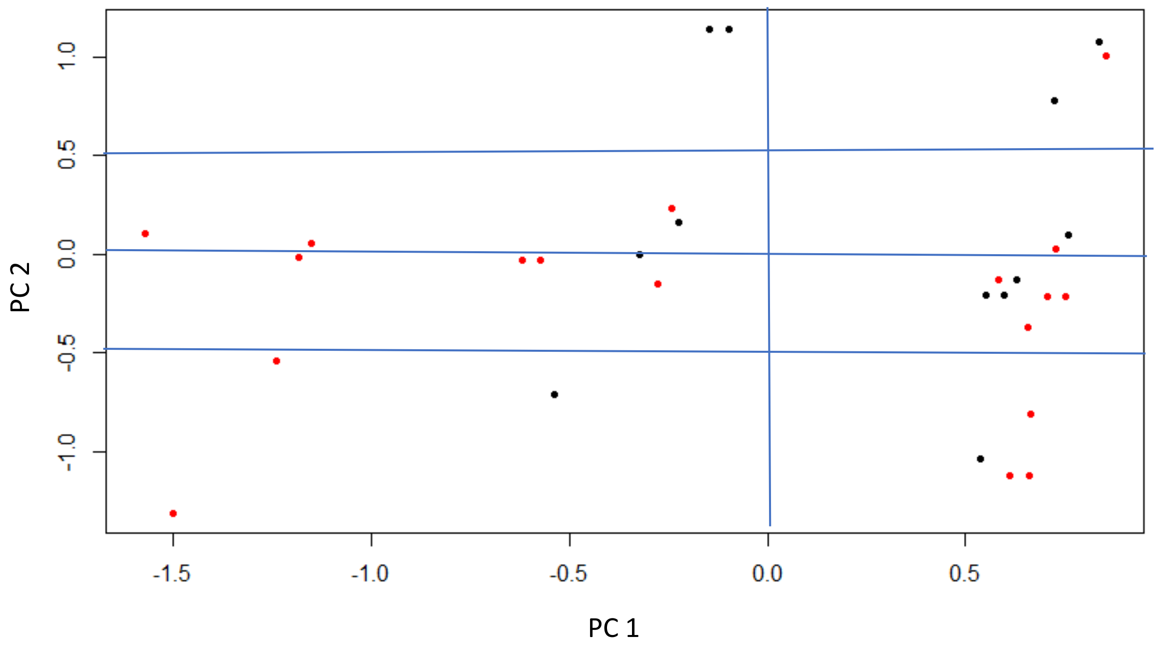


Figure 25: Principal component analyses separation of behaviour. A) Birds:MSA studies = 1-20. Primates:PSA studies = 21-40. B) Clear view of arrow trajectories and size. C) Birds:MSA studies = black nodes. Primates:PSA studies = red nodes.

4.3.3. Cluster Dendrogram - Behaviour

The cluster dendrogram for behaviour has more outliers than we see for the definition components indicating that the behaviours exhibited across primate and birds has some overlap. However, there is still a visible division between bird and primate studies with only 2 anomaly Birds:MSA studies (1 and 10) and 6 anomaly Primates:PSA studies (21, 27, 28, 29, 31 and 33).

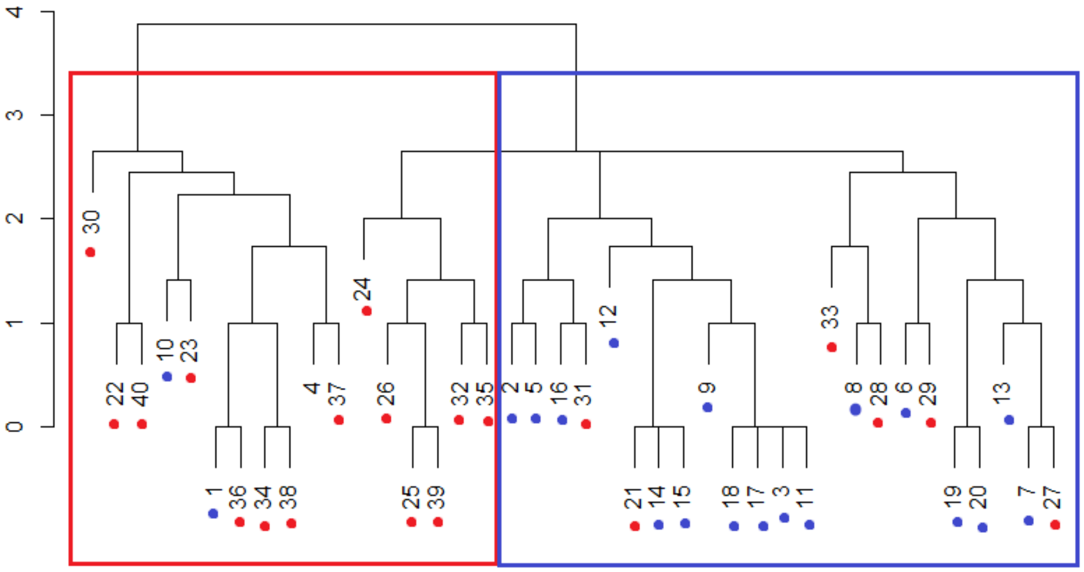


Figure 26: Cluster Dendrogram of behaviour. Birds:MSA studies = 1-20 (blue). Primates:PSA studies = 21-40 (red). Blue box = Birds:MSA best predicted split, red box = Primates:PSA best predicted split.

Table 12: Summary table of results

Figure/ Table	Approach	Result
Fig 4 (taxa)	Descriptive stats (taxa)	● Different taxa studies favour different terminologies. ● Inter-order studies are less likely to use key terminology. ● Interspecific and heterospecific terminology use is rare.
Fig 5	Descriptive stats (region)	● Relatively uniform terminology use across all regions. ● Fluctuation across terminology use is relative to overall biodiversity trends across the world.
Fig 6	Descriptive stats (Habitat)	● Terminology is proportionally evenly spread across habitat. ● Habitat has little influence over terminology choice.
overall	Descriptive stats	● Associative behaviour is apparent throughout the world across numerous habitats and species. ● Different studies use different terminologies. ● Terminology use is mostly affected by taxa.
Fig 7, 8, 9 Table 6	MCA – all studies	● Birds and Primates show slight opposing trends (Fig 7). ● Low explanation of variance is due to quantity and breadth of studies (Fig 8, Table 6). ● Chance and duration have the biggest impact on dimension 1 (Fig 9). ● Nuclear species is the anomaly and almost solely affects dimension 2 (Fig 7, 9).
Fig 10, 11 Table 7	PCA – all studies	● Both bird and primate trends are clearer (Fig 10). ● Explanation of variance increases slightly (Fig 11, Table 7).
Fig 12	PCA – all (terminology)	● Polyspecific association trend is parallel to primates. ● Other terminologies have an even spread.

Figure/ Table	Approach	Result
Overall		- Many species show no trend and reduce the explanation of variance. - There are differences between birds and primates' associative behaviour and/or in the way this behaviour is observed and defined. - PSA appears to use different defining criteria from other terminologies. - Provides justification to explore a smaller, refined dataset.
Fig 13, 14, 15 Table 8	MCA – reduced dataset (Primates:PSA and Birds:MSA)	- Higher explanation of variance (Fig 14, Table 8). - Primates:PSA pool towards the positive '1' variables, Birds:MSA pool towards unmentioned '0' variables (Fig 13). - 'Nuclear species' and 'Unequal benefits' are key defining characteristics in Birds:MSA (Fig 13, 15). - 'Chance', 'Duration', 'Interaction', and 'Complexity' are key defining characteristics in Primates:PSA (Fig 13, 15). - 'Proximity' and 'Benefits' are key defining characteristics in both (Fig 13, 15).

Figure/ Table	Approach	Result
Fig 16, 17, 18, 19 Table 9	PCA – reduced dataset (Primates:PSA and Birds:MSA)	• Higher explanation of variance (Fig 18, Table 9). • The definition fragments are more applicable in Primates:PSA as opposed to Birds:MSA studies (Fig 16, 17). • The most influential defining criteria for Primates:PSA are chance encounters (MC), duration (D), similar species (SS). • Nuclear species (N) and inequality of benefits (DB) are the most influential defining criteria for Birds:MSA. • Benefits and complexity are negligible when trying to ascertain the key differences between the 2 groups of data.
Figure 20	Cluster Dendrogram	• The Cluster Dendrogram predicts Primates:PSA and Birds:MSA split effectively with only 4 outliers (14, 22, 23, 26). • Only study 14 was wrongly classified using the additional discriminant function analysis.
Overall		• Reduced dataset provides a higher explanation of variance. • Primates:PSA gravitate towards the positive '1' variables especially 'Chance', 'Duration' and 'Interaction'. • Birds:MSA trend towards unmentioned '0' variables except for 'Nuclear species' and 'Unequal benefits'. • There are differences between birds and primates' associative behaviour and/or in the way this behaviour is observed and defined.

Figure/ Table	Approach	Result
Fig 21, 22 Table 10	MCA - behaviour	● Birds:MSA has 2 pools – centred around unmentioned (0) and opposing (-1) variables including not displaying agonistic behaviour or unified territorial defence but often travelled together (Fig 21, 22). ● Resting, foraging and travelling together; responding to each other's alarm calls; and low seasonality and temporal changes were common in Primates:PSA. ● There are many anomalies in the dataset, particularly in primates including agonistic behaviour and lack of coordinated travel.
Fig 23, 24, 25 Table 11	PCA – behaviour	● Much higher explanation of variance (Fig 23, Table 11). ● All variables seem to act mostly independently from one another (Fig 24). ● Seasonal and temporal change is a key defining characteristic for Primates:PSA. ● Agonistic behaviour is a key defining characteristic for Birds:MSA.
Fig 26	Cluster dendrogram - behaviour	● There are more outliers on the behaviour dendrogram indicating the Primates:PSA and Birds:MSA behaviour trends are more overlapping.

5. Discussion

5.1. Summary of Results

The results show extreme overlap in all terminology. However, some segregation is apparent around polyspecific associations suggesting that this behaviour may have unique features that differentiate it from other associative behaviours. Furthermore among taxa, primates were similarly distinguished from/ unique among taxa. This could suggest a unique behaviour exhibited by primates called polyspecific association. Nonetheless, cultural evolution and a lack of communication between fields (Dayton 1979; Heuschele et al. 2017) could have led to polyspecific associations having definition components that are so adapted to primates that the definition becomes too specific to use for describing associative behaviours in species outside the primate clade. For example, behaviours described as polyspecific included extremely social behaviours like grooming or other coordinated, interactive activities as part of their defining criteria (Pook and Pook 1982; Burton and Chan 1996; Porter 2001; Rehg 2006; Rehg 2017), as well as some defining proximity as being on the same tree rather than as a proportional unit of distance (Struhsaker 1981).

Despite the possible biases, the separation of primates and polyspecific associations from the rest of the terminologies and taxa required closer investigation to ascertain the key definition components of different terminology for associative behaviours. This was achieved by comparing Primates: polyspecific associations to the other group that showed uniqueness - Birds: mixed-species associations. Shrinking the dataset reduced the clustering and overlap in the multivariate statistics which contributed to the 16% increase in explanation of variance.

The separation of Primates: Polyspecific associations and Birds: Mixed species associations defining components is seen across all multivariate statistics. Bar 4 outliers, the dendrogram nicely shows the divide between Birds:MSA and Primates:PSA.

Studies on Birds:MSA were likely to have a nuclear species, and unequal benefits between the participating species as well as little aggression towards each other and a lack of unified territoriality. This subset largely trended towards unmentioned variables (coded as ‘0’) due to the lack of tested variables within the bird studies. Primates in polyspecific associations were likely to engage in coordinated activities together such as foraging, resting, alarm response and general interactions for a prolonged duration within proximity of each other. The associations were likely to occur beyond the expected chance encounters however many studies showed strong seasonality in the behaviour and sometimes antagonistic interactions between individuals from opposing species would occur. On average, were more behaviours that were both mentioned and occurred (coded as 1) in primate studies than in bird studies which can account for the tendency towards these categories.

MSA is a term that is used across a far wider spectrum of taxa than PSA. In order to be inclusive to the taxa, the definition may have been watered down which has led to vague, unclear definitions. This is further evidenced by the large percentage of studies that use the different definitions such as heterospecific, interspecific, mixed-species and polyspecific associations interchangeably within a singular study (Hino 1998; Windfelder 2001; Stensland et al. 2003; Srinivasan 2008; Desbiez et al. 2010). They are also often clumped together within definitions, for example ("mixed-species groups, also known as inter-specific or polyspecific" Heymann 2011; "polyspecific associations, also known as mixed species groups" Chapman et al. 2013).

Nonetheless, regardless of confusion and ambiguity a certain set of behavioural components were appearing frequently enough to establish a list of testable definition and behavioural components in which to compare studies and base definition recommendations on.

5.2. Researcher Differences

One of the biggest differences between studies was how the researcher approached the methodology. There was large variation in the variables that were recorded, the duration of the studies, the degree of manipulation and the analytical methods to ensure the interaction was purposeful.

Primate:PSA studies such as Buchanan-Smith (1999), Porter (2001), and Buzzard (2010) use long study durations to track seasonal fluctuations and help minimise observer disturbance as well as full day tracking to ensure uncommon behaviours were accounted for. They often used established methodology from previous researchers to ensure thorough data collection and many used Waser's gas model (1982) or similar alternatives to ensure an interaction was only identified as an association when it was more frequent than expected based on chance encounters. This contrasts immensely from Bird:MSA studies that often had instantaneous count data, shorter study durations, and inconsistent methods between studies. For example, Croxall (1976) would define as an association if they saw individuals of different species together for five minutes, Hino (2002) used a ten minute minimum duration and Hunt et al. (1988) opted against lengthy observations and used post-mortem catch data to ascertain likelihood of association between species. Many had to be discounted from the final dataset for manipulating the environment (Thompson and Barnard 1983; Berner and Grubb 1985; Goodale and Kotagama 2008) and overall there were far more gaps in both the definition segments and the behaviour variables.

The variation in recorded variables is evident from the magnitude of '0's within the overall dataset. The zeros were representative of a lack of acknowledgement of the definition segments within the paper. They were spread throughout the dataset and highlighted the 'thoroughness' of studies. Despite a slight tendency for primate studies to have less 'observation gaps' most still had a few variables that were overlooked. On the other extreme, many studies proceeded to categorise the behaviour they observed under the focus of associative terminologies with minimal recorded observation of the core definition segments that underpin this behaviour such as chance, duration and proximity. Gaps in tested variables makes it difficult to draw universal conclusions and compare studies against each other as well as reducing the validity of the terminology categorisation.

Physiological differences between species make it impossible to study all species in the same way. A fast submerged marine species provides far more prolonged observation challenges than a slow land mammal that's habituated to humans and has a small territory. Hence why many marine studies within the dataset used 'fishing catch data' as association justification (Au 1991; Das et al. 2000). However, technological advancement is creating more opportunities to overcome these difficulties remotely (Nowacek et al. 2016). This enables researchers to study all components of associative behaviour which will result in more complete and standardised data despite the physiological and ecological differences.

The range in which similar behaviour is displayed also requires researchers to make adjustments in methodology. Particularly elusive species are hard to observe for extended periods of time in-situ and the presence of a researcher creates behavioural responses in some species such as birds that may impact their true unaffected behaviour (Carey 2009). Thus researcher presence creates an environmental pressure that could lead to a disproportionate amount of associative behaviour in comparison to undisturbed habitat.

Researcher cultural bias often has a huge impact on the way a researcher views, records and categorises behaviours. This can occur due to our human psychology or our personal experiences. Species that display anthropocentrically recognisable social interactions are more likely to get categorised as gregarious (such as primates) and species that produce rare/ abnormal social cues often get overlooked, especially historically, despite the intention of the behaviour being the same (Schulz et al. 2008). This could partially explain why primate studies recorded more interactive behaviour during associations than studies on other species.

Researchers that studied the same species in the same places still sometimes used different methods and recorded different behavioural components. This may have been due to the bias of the researchers' own experience, existing knowledge and human error influencing the way they record their findings. The occurrence of this challenge is likely increased when there are no replicable guidelines to follow to minimise bias and error. In order to prove the validity of the behaviour categorisation, research methods should be standardised with all definition segments tested and recorded. This would eliminate all ‘0’s allowing for a truer reflection of trends within the dataset.

Researchers can use established understanding of behavioural cues for the species to ensure the research methods are inclusive. Try to minimise additional environmental pressure on the species which could create behaviour responses from species towards the researcher. Lastly reduce bias and error through following universal replicable method guidelines on observing associative behaviour between multiple species.

5.3. Differences between Taxa

There are many differences between the studies that lie far beyond the researcher's confusion of terminology. Fundamental taxonomic differences that have evolved over millions of years create the infinite variety of life on earth. Behaviours to complement species' unique genetic make-up evolve simultaneously alongside. As the tree of life continues to branch out, the variety and specialisms increase, making it exponentially harder for researchers to use the same standardised methods across all living species. The larger the breadth of species, the more variety you will have within the dataset, and therefore the more difficult it becomes to find underlying similarities using the same research methods.

This dataset was inclusive of all vertebrates totalling over 400 species (Appendix 1). The range of species spanned across 6 classes including 8 orders in Mammalia and over 15 orders in Aves. We can therefore conclude that the low explanation of variance in the datasets can be at least partially explained through biological and evolutionary differences in physiology and behaviour that often lead to unavoidable discrepancies in research methods.

5.4. Physiological Differences

There are countless physiological differences between taxa in this dataset that impact habitat/locomotion, diet, and predators. Physiological differences can also have a direct impact on how an associative behaviour is displayed or influence the species' behaviours that can in turn influence associative behaviour creating an indirect impact.

Birds and dolphins are found to associate but will only ever be able to stay in proximity to one another for limited durations as their physiology constrains them to autonomous habitats (Harrison 1979; Evans 1982). Birds will have to rest on land and many *cetaceans* swim at lower depths when not feeding. This physical limit on duration, proximity and therefore interaction will limit the recognition of these variables and consequently directly reduce the chance of this interaction being categorised as associative behaviour between species despite other variables in the same interaction providing contradictory evidence (Evans 1982).

Dietary adaptations influence social tolerance in animals, potentially also affecting tolerance to individuals of other species. For example, herbivorous diets tend to lead to greater tolerance than frugivorous diets because food is relatively abundant and not monopolisable (i.e. scramble rather than contest competition will prevail). A lack of contest competition with conspecifics may also create a tendency for passive tolerance towards non-specific individuals within close proximity (Pisor and Surbeck 2019). This increases the chances of multiple species occurring within proximity of each other for an extended period of time.

The diet of most birds in mixed species flocks were based on relatively valuable food resource requirements (such as insects and fruit) whilst diets of the primates commonly engaged in polyspecific associations were often low quality, i.e. non-vegetative plant matter such as leaves (*Colobinae*). Therefore, physiology of the primates exhibiting PSA creates behaviours/conditions that are far more conducive to group living than insectivorous, frugivorous and especially carnivorous species (Kinnaird 1992; Minta et al. 1992; Stensland et al. 2003; Brown 2013).

Predators of species can often vary extensively and this is also apparent in the birds and primates subset (Boinski et al. 2000; Hart 2000, 2007; Menezes and Marini 2017; Martínez et al. 2021). This initially is governed by the location of the associating species however in addition to this, physiological differences make birds and primates most attractive to different predator groups. Although raptor attacks were seen in both primate and bird studies many land predators such as big cats and chimpanzees were only mentioned as primate predators due to size and similar locomotive abilities (Hayward et al. 2006; Bugir et al. 2021) As the majority of reviewed studies mentioned predator avoidance as a driver for association between different species, the additional predatory pressure on primates could explain the increased prevalence and stability of variables within the associations.

5.5. Behavioural Differences

The physiological variation among species, ecological niches and environmental influences can all produce differences in behaviour among species. There are obvious behavioural differences between genetically distant species, but behavioural differences can be found within same class, order, and even different groups/individuals of the same species (Bshary and Noë 1997; Miller and Bain 2000). The range of different behavioural characteristics categorised under the four associative behaviour terminologies was large. It ranged from temporary foraging associations that included aggressive interactions as found in sheep and horses (Coates and Schemnitz 1994) to the permanent, stable tamarin groups that engaged in interspecific play and grooming (van Lawick-Goodall 1968; Peres 1992b). Some observations will inevitably have been misassigned and may not fit into the associative behaviour being reviewed within this paper. Nonetheless, there is a varied range of behaviours that are still correctly considered associative behaviour as the physiological differences mentioned above can lead to similar behaviours with the same intent being exhibited in very different ways.

One example is the differences in improving social bonds in primates and cetaceans. For many primates, social interactions will often involve physical contact such as allo-grooming as a way to improve social bonds (Dunbar 2010). Some cetacean species such as sperm whales (*Physeter macrocephalus*) improve social bonds though vocalisations by matching codas (Schulz et al. 2008). They produce the same outcome but the environmental variables will appear exceedingly different, for example less proximity is needed for vocal interactions. Distant interactions risk being overlooked in associations despite their social importance. The range of physiological and behavioural differences may warrant subsets within one encompassing definition of associative behaviour in order to accommodate the range of differences that have the same underlying intent whilst simultaneously be strict enough to filter out the studies that are currently misassigned.

In general, primates seemed far more likely to engage in coordinated activities with other species, such as foraging and resting together as well as responding to each other’s alarms, than birds. These differences seemed to mirror some of the typical differences between birds and primates' behaviour towards conspecifics. Many birds within the mixed species flocks are monogamous pairs rather than big groups (Terborgh 1990). Without the established social behaviours birds are far less likely to engage in these coordinated activities whilst in association with another species. Similarly, the inbuilt social tendency within the primate species is important when extending the sociality to other species (Goodale and Beauchamp 2010; Sridhar and Shanker 2014).

Interestingly one of the biggest impacts on the behaviour was the presence/absence of agonistic behaviour. Despite studies on bird associations generally providing less information on associative behaviours, many studies reported a distinct lack of discontent between the associating species. Birds can be aggressive towards each other however it is often towards an unknown individual rather than between bonded individuals (Hughes et al. 1997). In contrast, primates often display temporary agonistic behaviour towards individuals even within extremely gregarious conspecific social groups (Bernstein and Gordon 1974). These social behaviours are extended into associations and these behavioural differences could account for why primate associations were more volatile despite appearing more stable and complex. Birds and primates' behavioural differences in areas such as aggression and co-ordinated activities translates into their associations with different species causing divergent behaviour trends between the taxa.

5.6. Similarities

It is easy to see divergent trends and dissect the differences that cause disparities, especially between ornithology and primatology. Nevertheless, despite the differences, there are clear recurring themes throughout the dataset. All studies regardless of whether they were within the main trends had at least one of the definition variables (Appendix 1). Most studies identified multiple aspects of the association that fell within the core definition variables. By analysing the similarities between the subsets we can begin to see the wider picture of the behaviour and begin to answer some of the key underlying questions regarding the breadth and inclusivity of this specific associative behaviour. The consistency of associative behaviour from such a wide variety of taxa and the ability to deduce a set of recurrent variables within the dataset points to an underlying common behaviour that all taxa within the dataset are displaying. Similarly, diet, predators and behaviour patterns within associative species that occurs despite the variety of taxa helps us to understand that some species have adaptations that are more favourable to associative behaviour and thus are more likely, under the right conditions, to potentially associate.

Birds and primates were the only taxonomic groups to display a unique combination of consistent variables throughout the study. Each subset displays a clear set of ‘trademark behaviours’ via a unique composition of variables which can be recognised and categorised by a dendrogram analysis with high accuracy. This could mean they are different behaviours however due to the magnitude of overlap between variables within the studies, it is likely that they are subsets of an overarching behaviour.

Both primate and bird taxa are the most widely studied for this behaviour and associations have been found across a variety of locations in numerous species. The magnitude of available data may be a contributing factor to the ability to see trends within these taxa and with the magnitude of related studies increasing across other taxa, we may be able to see more unique subsets in the future.

5.7. Environmental Influences

All species have a set of delicate ecological requirements in order to be living at their optimum. If these requirements become unbalanced it can lead to environmental pressure on the species (Hoffmann and Sgrò 2011). If the pressure becomes too severe, the species must either adapt, move or die. Although ecological benefits to associating with other species is considered the main benefit of the associations, sometimes such behaviours only become established under harsh ecological conditions. Therefore, species may partake in associative behaviours as a by-product of less than ideal ecological conditions forcing species to adapt to coexist. This explains why many of the species do not engage in intense social interactions (Itzkowitz 1977; Hart and Freed 2003; Li et al. 2010). It also helps to explain why so many species split into monospecific groups for certain activities such as resting (Struhsaker 1979; Waser 1980; Porter 2001).

Due to global habitat degradation and reduction, many species' suitable habitats are shrinking (Powers and Jetz 2019). This is leading to greater geographical overlap among ecologically similar species as they retract to the few remaining suitable habitats. The current remaining habitats are also becoming less resource-rich leading to heightened competition and species forced to expand their diets leading to greater overlap with sympatric species. In this situation there are three options: fight until one species eventually dies out, adapt to live outside of the suitable habitat, adapt to live inside the suitable habitat with other species (Braunisch et al. 2008). Fighting takes a lot of energy and it is extremely risky especially for species without many defensive adaptations. Lost habitat is often claimed by urbanisation or agriculture making it extremely difficult to adapt to. The last option is to learn to associate with other species to survive together. This would often require limited interaction like we see in many studies and no evidence of the association if the environmental conditions are optimal. We also see this when the hunting/ predatory pressures are altered. This is witnessed in the red colobus. In Taï national park where red colobus, *Piliocolobus badius*, are hunted by chimpanzees, *Pan troglodytes* and the forest conditions are poor there is evidence of associative behaviour with diana monkeys, *Cercopithecus diana*. However in east African sites (such as Kanyawara in the Kibale national park) where chimpanzees less frequently hunt red colobus, *Piliocolobus tephrosceles*, (there are no or hardly any chimpanzees on Tiwai island where Kibale national park is based) and the forest conditions are better there is no evidence of associative behaviour of red colobus with the local *Cercopithecus* species (Bshary and Noë 1997).

With the world losing more habitat everyday (Powers and Jetz 2019), species rapid adaptation like creating associations can help species counter some of the stressors exacerbated by climate change (Hoffmann and Sgrò 2011). This hypothesis predicts that some of these associations will be a recent reflection of ecological pressure and we shall see more associative behaviour in the future unless there is habitat restoration. It also predicts that if we restore habitat we will see a reduction in associative behaviour. In order to monitor this change and confirm or falsify the hypothesis clear universal defining criteria of associative interactions will need to be followed.

6. Recommendations

6.1. A Unifying Framework for 'Association between Species' Terminology

The following are my suggestions on the defining criteria that should be included when researching associations between different species and which terminology to categorise the observed behaviour under. My suggestions are based on the findings from the reviewed studies and attempt to remove ambiguity and researcher confusion from the topic so that from here forward researchers have a standardised foundation from which they can continue to study the behaviour without the worry of misassignment of terminologies, lack of cross-field communication or cultural researcher bias.

It is imperative that all outlined variables (Table 13) are attempted to be recorded when studying this behaviour and reported on even if not found. All interactions and coordinated behaviour whilst in association should also be recorded. This will ensure a full systematic assessment of the association can be made, accurate categorisation into subsets can be considered and data can be collated and analysed effectively in the future to discover additional trends.

I propose removing the multiple terminologies that have similar overlapping vague meanings and sticking to one overarching terminology that is split into different subsets. This simultaneously removes the possibility of terminology bias between fields that researchers may miss during literature reviews, whilst creating clear distinction between studies that have used this criteria and those that haven't, allowing for a reliable review in the future and frees up the other terminologies enabling them to be used descriptively within the studies but not for definition purposes.

I suggest using 'polyspecific associations' as it is clear, unique and the descriptions used in publications that use this terminology describe the highest proportion of variables. It is also unlikely to get accidentally referred to in other studies such as 'mixed species associations'.

Polyspecific associations group 1 will refer to the encompassing definition. Some polyspecific associations that are able to be categorised in group one may also be able to be categorised into further groupings. Behaviour must be able to be categorised in group one before it can be considered for further grouping. Polyspecific associations group 2 will refer to the subset that the majority of birds:MSA currently falls under. Polyspecific associations group 3 will refer to the subset that is currently mostly dominated by primates. As the criteria guidelines require record of all variables there will be no reference to the not mentioned variables (‘0s’). If more suitable subsets are found through future reviews then more groups can be proposed and added.

Table 13 - Research guidelines for the essential and recommended variables to observe and record whilst studying polyspecific associations.

Variable	**PSA1**	**PSA2**	**PSA3**	**PSAn**	**Research Guidance**
Different species	x	x	x	x	Ensure there is more than one genetically distinct species in association.
Proximity	x	x	x	x	Establish suitable relative ‘close’ proximity based on species behaviour andexisting literature. 2+ individuals of different species must be within this to record observations.
Duration	x	x	x	x	Record total duration within ‘close’ proximity. Gaps must be noted and omitted from total duration.
Chance	x	x	x	x	Apply findings to Waser’s Gas Model to ensure the observation was not a chance encounter.
Nuclear species		x			One or more species that are sought out due to an attractive characteristic(s) they have.
Interaction/ coordinated activity	1	1	3	1	The number refers to the amount of different interactions/coordinated activities (from observered variables list) must be observed between individuals of different species within the association. Non-antagonistic.
Suggested list of coordinated activities.					**Research Guidance**

Alarm Response	Species A reacting to an alarm call made by species B whilst in association.
Defence	Defending shared territory or resources together from threat. Shared territory can be temporary.
Forage	Engaging in foraging activity. Can include hunting and eating.
Rest	Appearing stationary without foraging. Engaging in no other activity. Can include sleeping and roosting.
Travel	Moving in the same direction whilst sustaining relatively close proximity that considers differences in locomotion.
Suggested list of interactions	**Research Guidance**
Play	Species A attempts to initiate play behaviour/signals to species B.
Mate	Species A displaying any form of sexual behaviour or courtship shown to species B.
Groom	Species A attempting to groom species B. Can include gleaning.
Supplementary criteria to record	**Research Guidance**
Benefits	The benefits each species seem to receive from the association. Note any inequality of benefits.
Antagonistic interactions	Any hostile interactions between species including fighting, warnings, and vocalisations.
Seasonality	Record any fluctuations in associations according to daily, monthly or annual cycles.

6.2. Polyspecific Associations – Group 1 (PSA1)

The encompassing definition for PSA1 needs to cater for the range of different physiologies and behaviours that share a function however be strict enough to filter out behaviour such as random encounters, anomalies or a different behaviour entirely.

For this reason all associations under PSA1 must mathematically prove the association occurs more than expected by chance. I have suggested using Waser's Gas Model (1982) to determine whether encounters are more frequent than expected by chance, as it is an established and refined equation that, due to its relative proportional considerations, is inclusive of all species and specifically targets the possibility of chance encounters between two species seemingly in association with one another. This will entail all species to be within a suitable proximity of one another for a proportional duration. Other methods may be more suited for species that do not have strict territories, as the weakness of the Waser gas model is that it assumes that territories are circular and can be considered if appropriate.

Proportionally 'close' proximity and 'prolonged' duration must also occur to meet the criteria of PSA1. 'Close' proximity can be at the researcher's discretion on a case-by-case basis; however this number must be a true reflection based on previous literature and current observations. The duration of sustained proximity should be recorded in order to successfully demonstrate non-random occurrence. Therefore, when prolonged observations cannot be reliably made by foot, technology must be implemented to ensure an accurate timescale of association can be built as this is a fundamental aspect of associative behaviour.

Perhaps the most obvious variable that must be true to categorise as PSA1 is that it has to be with two or more distinct species otherwise it should be categorised as standard associations/ group living.

Finally there must be evidence of some non-antagonistic interaction or co-ordinated activity. This can include any of the behavioural variables and can be discretionary based on both species' existing behaviours. As habitat degradation increases more species will be forced to share territories, space and resources with each other. Therefore this criterion is to further prove the intent of the association rather than a passive encounter around a common resource or habitat.

The rest are not essential to categorise as PSA1 however must still be checked and recorded as they are all established components of polyspecific associations and are used to define and categorise the other groups. They also ensure no gaps are left in the datasets so future reviews can potentially propose new subset groups. A full list of variables, justifications, suggested research methods and groupings can be seen in Table 13.

6.3. Polyspecific Associations – Group 2 (PSA2)

For an association to be categorised as PSA2 it must first meet all the criteria for PSA1. In addition, there must be evidence of a nuclear or core species. This species is consistently present within the associations and are sought out by the other species due to an attractive characteristic they hold, for example good sentinels. For this reason the benefits are often unequal so associations can still be categorised as PSA2 if the association seems somewhat commensal. The individuals must not exhibit hostility between each other however they do not need to share in extensive activities beyond that which are required for PSA1 such as defending shared territory.

PSA2 is much the same as PSA1 except for the unique defining characteristic of a nuclear 'core' species that attracts other species into association often creating clear inequality in received benefits. These associations should remain largely non-antagonistic at a similar proportion to seen in conspecifics.

6.4. Polyspecific Associations – Group 3 (PSA3)

PSA3 is the most socially interactive of all groups. The range and type of coordinated behaviour is the unique defining criterion within this subset. On top of meeting all PSA1 essential criteria, associations within PSA3 must exhibit multiple behavioural interactions and coordinated activities. They must be observed participating within proximity as seemingly in union for at least 3 daily activities including foraging, travelling, resting, defending territory and responding to each other's alarm calls. Ideally, there should also be a direct social bonding activity between individuals from opposing species such as play, grooming, mating, call and response, alloparental care. Though not essential it is encouraged to seek and record these interactions as it adds merit to species integration and mergence into a coordinated functioning unit parallel to their single species counterparts.

PSA3 contains associations that not only come together to reap the benefits of each other but once formed act as a unified group that perform activities together and interact with each other akin to how they are known to behave with members of the same species as them.

6.5. Polyspecific Associations – Group n (PSAn)

Other subsets may be added in the future if new trends appear after following this inclusive approach to polyspecific associations. I shall refer to these as PSAn. In order to add another group, there must be substantial significant evidence from multiple studies and researchers. PSAn must still meet all the defining criteria required for PSA1 as well as contain unique characteristics that are distinct from PSA2 and PSA3. Finally, the new criteria in PSAn must be able to be translated across all species to ensure the characteristics are not based on taxonomic specialities.

6.6. Polyspecific Associations – Final Definition

Polyspecific associations (PSA1) occur when two or more species are within close proximity to each other for a duration that is longer than expected in chance encounters. Whilst associating, the species engage in at least one non-antagonistic interaction or co-ordinated activity together.

The association can develop to contain nuclear species (PSA2) or to form a unified group that performs multiple coordinated activities and social interactions together akin to their single species counterparts (PSA3).

7. Conclusion

To conclude, throughout the studies there has been a vast amount of behaviour categorised under the four main terminologies (polyspecific, heterospecific, interspecific and mixed species) that describe associations between two or more species. These examples were found across the globe in multiple habitats in numerous species. When the defining components for the behaviour are looked at closely, we can see large variance in the variables reported from study to study. Many studies using the same terminology record contrasting behaviours and studies with an identical composition of variables used different terminologies. The low explanation of variance in the correspondence and component analyses can be partly explained by the ambiguity surrounding the definitions of the terminologies leading to researcher confusion and ultimately misassigned definitions. There are also differences in physiology, behaviour and methodology approaches that contributed to the extensive recorded variance among studies.

Despite the differences, there was a clear set of definition component variables that over-arched in various combinations across all studies. These included: interaction, prolonged duration, close proximity, benefits to both or at least one species, at least 2 different species which can be similar, presence of a nuclear species and lastly occurrence beyond chance encounters. This points to the studies all finding a single encompassing associative behaviour that requires species to display some of these variables.

There were two clear trends throughout the dataset that separates primates: polyspecific associations and birds: mixed species associations. When analysed closer they were found to abide by their own unique combination of variables within the overarching definition components. Birds in mixed species flocks were likely to have a nuclear species, and unequal benefits between the participating species. Primates in polyspecific associations were likely to engage in general interactions together for a prolonged duration within proximity of each other. The associations were complex and likely to occur beyond the expected chance encounters.

The birds: mixed species associations and primates: polyspecific associations subsets extended further into behavioural components. Birds in mixed species flocks displayed very little aggression towards each other and a lack of unified territoriality. Primates in polyspecific associations were more likely to engage in coordinated activities together such as foraging, resting, alarm response. These associations had strong seasonality and sometimes antagonistic interactions between individuals from opposing species would occur.

An alternative hypothesis is that species will only associate with each other if there are significant environmental pressures that are forcing such adaptation. However, this may only happen if the species have already evolved behaviours such as gregariousness and low cross-species territoriality that are favourable in associations between different species thus providing a predisposed advantage.

Without revisiting every study sample with a new set of standardised criteria to eradicate all the unmentioned variables (‘0s’), it is impossible to truly answer whether these studies have found the same behaviours displayed (by the species or recorded by the researcher) in different ways (through natural or cultural evolution) or whether they are different behaviours wrongly categorised as the same ambiguous terminologies. It is difficult to tell without further investigation whether the two main subsets were driven by taxonomical or terminology differences and whether they should fall into subsets of an encompassing definition or stand alone as unique behaviours in their own right.

Regardless of the unknowns, it is clear that this area of research needs to enter into a new paradigm with a standardised set of universal defining criteria so that researchers can begin to look more thoroughly at the true breadth and characteristics of associations between different species.

The suggested recommendations create clear defining criteria for a single terminology that is thorough and easy to follow. It provides clear baseline components that can be welded to create a strong encompassing definition for polyspecific associations unbiased across all taxa. It includes distinguished subsets within the behaviour to ensure special trends are recognised and offers the space for justified additions in the future. The recording guidelines are inclusive of all components found across the studies to ensure future observations don’t have some of the gaps that make the current studies so difficult to collate.

If followed, these definitions and guidelines could create a new paradigm of how we approach associative behaviour and allow us to accurately record and define polyspecific associations in a comparable way that ensures we can truly grasp the universal breath and collective complexities of this fascinatingly intricate behaviour.

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