



The native and exotic prey community of two invasive paper wasps (Hymenoptera: Vespidae) in New Zealand as determined by DNA barcoding

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Abstract Social wasps are invasive in many regions around the world. In their new communities, introduced predators such as these wasps may be beneficial as consumers of exotic pests, but they will also consume native species. Here, we examined the diet of the exotic European paper wasp (*Polistes dominula*) and the closely related congener, *Polistes chinensis*, in a region of New Zealand where they co-occur. DNA barcoding was used to analyse their diet. The diet of both wasp species was largely Lepidopteran but other orders such as Hemiptera, Diptera and Coleoptera were also represented. Our analysis showed substantial site-to-site variation in diet. The two wasps differed significantly in their prey, although these differences appear to be driven by taxa identified from a small number of DNA reads in a small number of samples. Native and introduced fauna were represented in the diets of both wasps and included important agricultural pests. Of the 92

prey taxa able to be identified to species level, 81 were identified as exotic or introduced to New Zealand. The remaining 11 were species native to New Zealand. However, our estimates suggest over 50% of the prey DNA in the wasp diet is derived from native species. These wasps are abundant in some coastal and urban habitats, where they are likely to consume pest species as well as native species of conservation importance. The ecosystem services or costs and benefits provided by these invasive species are likely to be contingent on the prey communities and habitats they occupy.

Keywords Exotic predators · Vespidae · Diet · Cytochrome c oxidase subunit I · Ecosystem services · Conservation

Introduction

Exotic species can have both beneficial and harmful effects on their recipient communities. While exotic species can act as competitors for native organisms, they can also provide benefits to the ecosystem such as pollination, providing habitat and acting as an additional food source (Pawson et al. 2010; Pintor and Byers 2015; Stavert et al. 2018). The introduction of exotic species can act to increase biodiversity, which has been linked to increased ecosystem stability and reduced invasibility (Tilman 1999; Eisenhauer et al. 2013). Exotic species that become invasive can exert

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negative pressures on recipient ecosystems, however, through competition for resources and direct predation of native species (David et al. 2017).

Predatory invertebrates can have significant impacts on native fauna (Crowder and Snyder 2010). These impacts are arguably most apparent in social wasps in the Vespidae family, whose adaptive behaviours and ability to reach substantial population densities make them particularly effective invasive predators (Beggs et al. 2011; Lester and Beggs 2019). Invasive wasps have repeatedly been shown to exert considerable predation pressure on recipient communities (Toft and Rees 1998; Beggs and Rees 1999; Wilson et al. 2009; Parent et al. 2020). These wasps, however, can also be beneficial for their recipient communities. Aculeate wasps can act as biological indicators and perform important ecosystem services as parasites, predators, pollinators, decomposers and seed dispersers (Brock et al. 2021).

Polistes dominula is a paper wasp species that was found in New Zealand in 2016 (Ministry for Primary Industries 2016). The predatory nature of *P. dominula* has been shown to threaten native species in its invaded range (Baker and Potter 2020; McGruddy et al. 2021b). Due to its recent arrival in New Zealand, it is not yet known how the establishment of *P. dominula* will affect local entomofauna. Identifying what this invasive wasp is feeding on in New Zealand may provide insights into how it will impact biodiversity. New Zealand does not contain any native paper wasps though two other species have been introduced, *Polistes humilis* and *Polistes chinensis* (Clapperton et al. 1989), the latter being the most widely distributed and found on both the North and South Islands (Clapperton and Dymock 1997). *Polistes chinensis*, like other *Polistes* species, is considered a significant predator of lepidopteran (butterflies and moths) larvae (Clapperton 1999; Ward and Ramón-Laca 2013) though other groups are represented (Kudo 1998, 1999). *Polistes dominula* has similarly been shown to feed on Lepidoptera (Stamp and Bowers 1988; Rayor et al. 2007; McGruddy et al. 2021b), however, it has been suggested that this species has a more generalist diet than that of other paper wasp species (Cervo et al. 2000; Schenk and Bacher 2002). In New Zealand, *Polistes* spp. have been shown to prey on both native and introduced species (Ward and Ramón-Laca 2013; Lefort et al. 2020). The presence of *P. dominula* could add to the threats that New Zealand's

native invertebrates face, although it could also act as a natural biocontrol for other current and new invasive pests. *Polistes* spp. have also been considered for biocontrol of agricultural pests due to their heavy predation of butterfly and moth larvae, which feed on various crops (Oliveira et al. 2017; Southon et al. 2019).

Investigating species' diet contents historically involved searching through diet samples, visually inspecting and identifying prey (Kasper et al. 2004; Parent et al. 2020). These methods are time consuming and not always accurate. With the advent of High-throughput DNA sequencing technology, it is now possible to inspect diets more thoroughly using DNA barcoding. This technique involves sequencing a conserved gene that contains species-specific signature sequences. The process consists of collecting a diet sample, such as gut contents or faecal matter, from a target species. Selected universal primers are then used in the polymerase chain reaction (PCR) to target the specific gene homologues (Valentini et al. 2009). Genes that are conserved across a wide range of species, such as cytochrome c oxidase subunit 1 (COI), are often used in DNA barcoding studies (Hebert et al. 2004; Steinke and Hanner 2011; Wirta et al. 2015; Cheng and Lin 2016; Turanov et al. 2016; Ayesha et al. 2019). The COI mitochondrial gene is an ideal candidate gene for DNA barcoding as it has been conserved across many taxonomic groups yet has enough variation to allow for the identification of organisms to the species level (Hebert et al. 2003). High-throughput DNA sequencing enables the identification of many different species in a single diet sample. This technique has been used widely for both vertebrate (Zeale et al. 2011; Lyke et al. 2019; Takahashi et al. 2020) and invertebrate taxa (Paula et al. 2016; Nakano et al. 2017; Lafage et al. 2019) to analyse and compare the diets of different species.

Our goal in this study was to use DNA barcoding to describe and compare the diets of both *P. dominula* and *P. chinensis* in a region of New Zealand where both species overlap. We sought to identify differences in diet composition and prey range to investigate potential prey overlap between the two predators and their impact on local fauna. We were particularly interested in the contribution of native and introduced species in the diets. Using these wasps as a case study we aim to investigate the relative diet of these predators, to provide an indication of these invasive

species' contribution in providing beneficial ecosystem services (such as for biological control) or as pests of conservation importance (e.g. by consuming rare species).

Methods

Study region and wasp larvae sampling

Larvae of *P. dominula* and *P. chinensis* were collected across nine locations near the city of Nelson, New Zealand (Supplementary Fig. 1) over the 2019/2020 summer. These locations were confined to coastal areas within 200 m of the ocean. Vegetation consisted largely of shrubs with some small trees, representing recovering native coastal vegetation. The composition of plant species was mainly *Myoporum* spp., *Coprosma* spp., and *Muehlenbeckia* spp., however, the stage of restoration of these sites varied. At some sites, vegetation was well established while others had recently been planted, likely influencing wasp and prey species compositions. Sites were located a minimum of 700 m from each other, which is regarded to be further than the typical foraging distance of other *Polistes* spp. (Suzuki 1978; Parent et al. 2020).

In November 2019, areas of approximately 1000 m² were surveyed for the presence of paper wasp nests at each of the nine locations (Supplementary Fig. 1). A site was considered to be dominated by one species if over 80% of nests found belonged to one species. Where this was not possible the nests of other wasp species were physically removed from within the 1000 m² area. Monitoring of species prevalence continued every month over four months until February 2020. In all, there were three sites of approximately equal *P. dominula* and *P. chinensis* occupation, three sites of predominantly *P. dominula* occupation, and three sites of predominantly *P. chinensis* occupation. These sites were created to represent sympatric and allopatric populations of each wasp species and were therefore non-randomly selected. Both species were sampled at sites with approximately equal abundances of wasp species. At the single-species dominant sites only the most abundant wasp species was sampled.

Individual wasp larvae were removed from live nests using forceps. Fourth and fifth instar larvae

were selected and placed in a solution of 90% ethanol for storage at $-18\text{ }^{\circ}\text{C}$ until dissection and DNA extraction. Wasp larvae were chosen as they are fed material by the adult foragers. Prey material is consumed by the larvae and retained in the gut until pupation. The largest and oldest larvae were sampled as these contain the most material in their gut. Forceps were rinsed and sterilised in an ethanol solution between each sampling event. One larva was removed from each of three nests for each species at respective sites. This process was repeated over three months from December 2019 until February 2020. Samples were thawed slightly before dissection. The guts were removed under a dissecting microscope and placed in a vial with 100% ethanol and stored at $-80\text{ }^{\circ}\text{C}$ until DNA extraction. In total 102 *Polistes* gut samples were prepared for DNA extraction and further analysis.

DNA extraction, amplification, sequencing and taxonomic assignment

DNA was extracted using a similar approach to Loope et al. (2019). Each gut sample was mechanically homogenised in a Precellys Evolution homogeniser (Bertin Technologies, France) with two stainless steel beads, 1 mL GENEzol DNA Plant Reagent (Geneaid, Taiwan) and 5 μL β -mercaptoethanol per tube. Chloroform isoamyl alcohol was used to isolate DNA. Isopropanol was used to precipitate the DNA, which was then purified with a 70% ethanol wash and resuspended in 100 μL nuclease-free H₂O. DNA concentrations were measured using a NanoPhotometer NP80 (Implen, Germany). Sample PCR amplification and DNA sequencing was provided through Custom Science (Auckland, New Zealand) and NovogeneAIT Genomics (Singapore). PCR primers targeting mitochondrial gene, COI, developed by Zeale et al. (2011), were used (ZBJ-ArtF1c: AGATATTGGAACWTTATATTTTATTTTTGG and ZBJ-ArtR2c: WACAATCAATTWCCAAATCCTCC). These taxon-specific primers amplify a 157 base-pair (bp) region and have been successfully used to identify arthropod prey in bat faecal samples (Zeale et al. 2011; Alberdi et al. 2020). Of the 102 *Polistes* gut samples, 58 amplified successfully (30 *P. dominula* and 28 *P. chinensis*) and were sequenced on a HiSeq platform (Illumina, USA) generating 150 bp paired-end reads.

Taxonomic assignment was performed using Basic Local Alignment Search Tool (BLAST) searches in the National Center for Biotechnology Information (NCBI) non-redundant nucleotide database (nt) to generate Molecular Operational Taxonomic Units (MOTUs). Where possible, MOTU sequences were identified to species level. As we cannot rule out that a single MOTU represents multiple species they are presented as the genus name followed by the “spp.” qualifier (for example “*Lycaena* spp.”). Most alignments were clustered around 157 bp, the expected length of the amplicon generated by the COI primers (Zeale et al. 2011). To increase the confidence in the accuracy of the MOTU identification and reduce false positives, only those for which alignments exceeded 100 bp long were retained for analysis. MOTUs with BLAST matches less than 98% percent identity were removed, as well as those with less than 10 sequences retrieved from a sample (Vesterinen et al. 2018). Reads identified as belonging to *Polistes* spp. were filtered out prior to analysis as these reads are likely from remaining tissue from the wasp larvae rather than from their diet. Supplementary Table 1 was constructed using these remaining reads as an overall diet community. Presence-absence data were used to reduce the impact caused by recovery bias during DNA amplification and sequencing (Pompanon et al. 2012). For taxa successfully identified to species level, their biostatus was determined using the New Zealand Organism Registry (NZOR) as well as the Global Biodiversity Information Facility database (GBIF). For statistical analyses, this prey taxa community was further filtered on the basis of relative read abundance, keeping MOTUs that represented at least 1% of the reads in a gut sample (McInnes et al. 2017). This approach has previously been shown to reduce the likelihood of over-estimating the importance of rarer taxa to the diets of each species (Deagle et al. 2019). By presenting both diet communities, an estimate of the full breadth of each species’ diet can be shown while not impacting the validity of statistical analyses.

Data analysis

To assess the completeness and diversity of each wasp diet, species accumulation curves were constructed using the ‘speccaccum’ function in the ‘vegan’ package (Oksanen et al. 2019) in R version 4.0.2 (R Core

Team 2020). While fitting these curves, the rarefaction method was specified to show how the mean diversity of taxa found in each wasp’s diet increases with sample size. Species accumulation curves are steep to begin with as common taxa are observed quickly, eventually plateauing as fewer, rarer taxa are added with increasing sample sizes. The flatter the curve, the closer our samples are to representing a complete paper wasp diet at our study site. Overlapping curves indicate a similar diversity of taxa within each predator’s diets while non-overlapping curves may indicate that one species is more generalist than the other.

A Permutational Multivariate Analysis of Variance (PERMANOVA) test using Bray Curtis indices was performed using the ‘vegan’ package (Oksanen et al. 2019) in R version 4.0.2 (R Core Team 2020). This analysis was run using the subset of taxa that made up over 1% of reads in a sample. The relative read abundances of the MOTUs in this subset were set as the dependent variables. Wasp species, site and month of sample collection were set as independent variables. The number of permutations was set to 9999.

In addition, MOTUs identified from samples of both species from sympatric and allopatric sites were plotted as Venn diagrams to visually assess the dietary overlap of both species. To test for differences in dietary overlap between different site conditions a two-sample test of no difference in proportions was used. For all statistical tests, significance was considered at $p < 0.05$.

Results

DNA sequencing identified a total of 29,233,868 reads across 58 samples (30 from *P. dominula* and 28 from *P. chinensis*). After filtering out reads identified as belonging to *Polistes* spp., 7,615,211 of the reads remained. Reads were also removed if they had a match percent identity of less than 98%, were shorter than 100 bp, or if there were fewer than 10 reads retrieved from a sample, leaving a total of 3,526,151 DNA reads. These corresponded to 123 distinct MOTUs representing 8 taxonomic orders, 27 families, 93 genera with 92 identified species (Supplementary Table 1).

Across all samples from both species, 109 of the 123 MOTUs were taxa within the order Lepidoptera.

Lepidoptera was the most represented order across all wasp samples and was found in all gut samples of *P. dominula* and in 26 (93%) *P. chinensis* samples (Fig. 1). Despite only two of the 123 MOTUs belonging to the order Hemiptera (true bugs), these taxa were found in 22 (73%) samples from *P. dominula* and 14 (50%) from *P. chinensis*. Diptera (flies) was the second most represented order in terms of diversity of taxa, with five of the 123 MOTUs belonging to this group. Dipterans were found in 13 (43%) samples from *P. dominula*, and nine (32%) samples from *P. chinensis*. Other orders represented in both species' diets included Araneae (spiders), Mantodea (mantids) and Coleoptera (beetles). Taxa from the orders Orthoptera (crickets, wētā and grasshoppers) and Hymenoptera (ants, bees and wasps) were identified exclusively from *P. dominula* samples.

Of the 3,526,151 reads, 3,195,215 DNA reads were tentatively identified to species level and as belonging to the 92 MOTUs. Of the 92 MOTUs identified to species level, 81 were identified as exotic or introduced to New Zealand. The remaining 11 were identified as species native to New Zealand. However, of the 2,667,854 reads retrieved from *P. dominula*

samples identified to species level, 57% were the identified as DNA belonging to 10 of the native species. Of the 527,361 reads retrieved from *P. chinensis* samples, 52% were the DNA of 10 native species.

Forty-eight of the 123 MOTUs identified (note that we were able to tentatively identify only 92 of these to species level, as above) were found to make up over 1% of reads in any given sample (Supplementary Table 2). A number of native and introduced taxa were identified in the diets of both wasps. The most highly represented native taxa in the diets of *Polistes* spp. were species of southern blue butterflies (*Zizina oxleyi*), variable cicada (*Kikihia muta*), owl moths (*Ectopatria aspersa*), dark sword grass moth (*Agrotis ipsilon*) and leaf roller moths (*Holocola* spp.). Non-native taxa included sugarcane army worms (*Leucania stenographa*), apple looper moths (*Phrissogonus laticostata*), slender burnished brass moth (*Thysanoplusia orichalcea*), and emperor gum moths (*Opodipthera eucalypti*). Some of these introduced taxa include agricultural pests such as the light brown apple moth (*Epiphyas postvittana*) and the cosmopolitan army worm (*Mythimna separata*). Interestingly, a species of fly (*Trigonospila brevifacies*) was identified in the diet of *P. dominula* which was imported to New Zealand as biocontrol for invasive pests such as the light brown apple moth (Shaw et al. 2001). Other parasitic taxa that were present were biting midges (*Forcipomyia* spp.) and Braconid wasps (*Diolcogaster* spp.), which together with *T. brevifacies*, may have entered the diets of these wasps through parasitised prey. Some taxa that were identified in this study were not listed as present in New Zealand within the New Zealand Organism Registry. New Zealand entomofauna has many understudied groups (New and Samways 2014) so it is likely that these taxa do not have sequences in the NCBI database. In this case, the closest DNA match on the database may then be used and the MOTU identified as an organism not known to occur in New Zealand. If the MOTU meets all other requirements outlined in our methods then there is no reason to remove it from the results.

When accumulation curves were plotted using the full range of MOTUs identified in wasp larvae, *P. dominula* samples contained slightly higher diversity of MOTUs than *P. chinensis* samples; however, this was not statistically significant (Fig. 2). This pattern was further confirmed when analysis was repeated

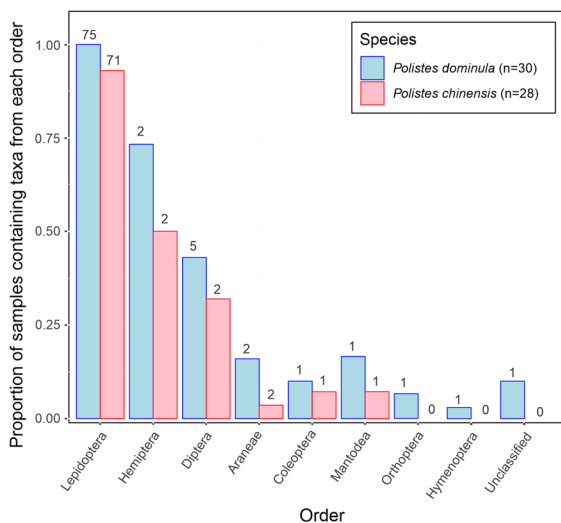


Fig. 1 Proportion of samples that contained prey taxa from each order, across all sites. The x-axis shows the orders that were represented in the diets of the wasps while the y-axis is the proportion of samples that contain at least one taxon that belongs to the order. Numbers above each bar show the number of taxa from each order identified in the diets of each wasp species. *Polistes* spp. reads were excluded prior to this analysis, thus Hymenoptera refers to non-*Polistes* taxa

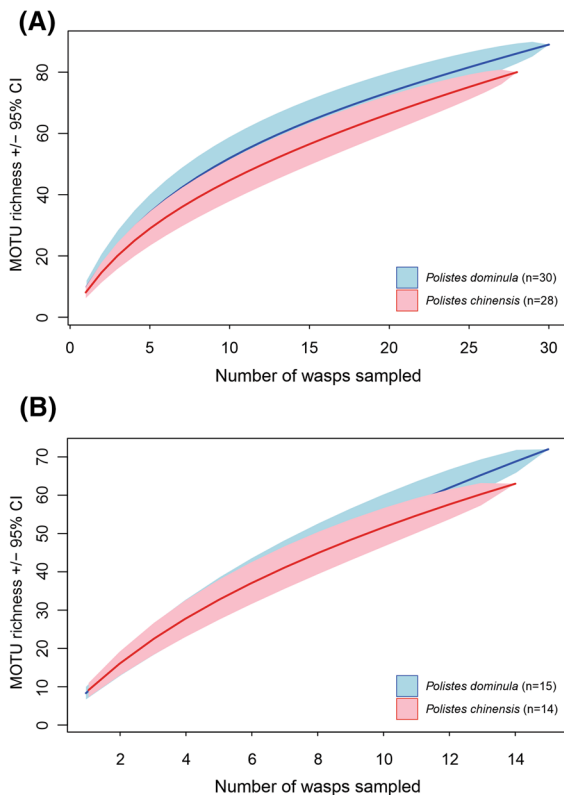


Fig. 2 Accumulation curves fitted using the rarefaction method showing the number of unique MOTUs ($\pm 95\%$ CI) expected to be found in increasing numbers of wasps sampled at all sites (a), and at sympatric sites only (b). Although the accumulation curve of *P. dominula* is consistently higher than that of *P. chinensis*, the confidence intervals overlap indicating no significant difference in prey diversity

only considering samples from sympatric sites. The two curves overlapped considerably indicating the two species diets did not differ in prey diversity. The species accumulation curve did not reach a plateau for either wasp species, suggesting that additional taxa are likely to be present in the diets of both wasps.

PERMANOVA found the interaction between wasp species and site to be significant (PERMANOVA: $F=1.700$, $df=2$, $p\text{-value}=0.027$), suggesting that while prey assemblages differed from site to site, the diets of the two wasp species also differed significantly. We investigated whether there was any effect due to the date of when larvae were sampled, by including a term that represented the month of sample collection. Month of collection was not statistically significant, however (PERMANOVA: $F=0.928$,

$df=2$, $p\text{-value}=0.541$). This result is likely due to the low number of comparable samples across species, sites and months rather than a true reflection of foraging patterns.

Across all sites, of the 123 unique MOTUs that were identified, 89 (72%) were found in *P. dominula* samples while 80 (65%) were identified from *P. chinensis* samples. In terms of diet overlap, 46 MOTUs were present in both *P. dominula* and *P. chinensis* diets. This suggests a significant amount of dietary overlap between the two species with both wasps having over 50% of their prey items in common (Supplementary Fig. 2). Similar amounts of overlap are apparent when considering only samples collected from sympatric and allopatric sites. For the MOTUs identified from wasp samples in sympatric sites, 72% (72/100) were found in *P. dominula* samples with 63% (63/100) identified in samples from *P. chinensis*. Overlapping taxa consisted of 35 MOTUs, with *P. dominula* and *P. chinensis* sharing 49% and 56% of their prey with the other species respectively (Fig. 3). Similarly, of the MOTUs identified from wasp samples in allopatric sites, 80% (53/66) were found in *P. dominula* samples with 62% (41/66) identified in samples from *P. chinensis*. Overlapping taxa consisted of 28 out of 66 MOTUs, with *P. dominula* and *P. chinensis* sharing 52% and 68% of their prey with the other species respectively (Fig. 3). The proportion of prey taxa in common in these allopatric sites was higher than in sympatric sites though not significantly different (two-sample test of no difference in proportions: $z=1.146$, $p\text{-value}>0.05$).

Analysis of diet compositions in terms of the relative read abundance suggested that the differences were quite small. When looking at all of the DNA reads retrieved from each species of wasp, it was possible to see the proportion of reads that each MOTU makes up across all samples. In all, 2,971,737 DNA reads were retrieved from *P. dominula* samples and assigned to one of the 123 MOTUs. Over 99% of these DNA reads were assigned to MOTUs that were also found in *P. chinensis* samples. Similarly, of the 554,414 DNA reads retrieved from *P. chinensis* samples and assigned to one of 123 MOTUs, over 99% were identified as belonging MOTUs also found in *P. dominula* samples. MOTUs found exclusively in *P. dominula* diets made up less than 0.5% of DNA reads retrieved from *P. dominula* samples. In the case of *P. chinensis*, less than 0.8% of reads extracted were

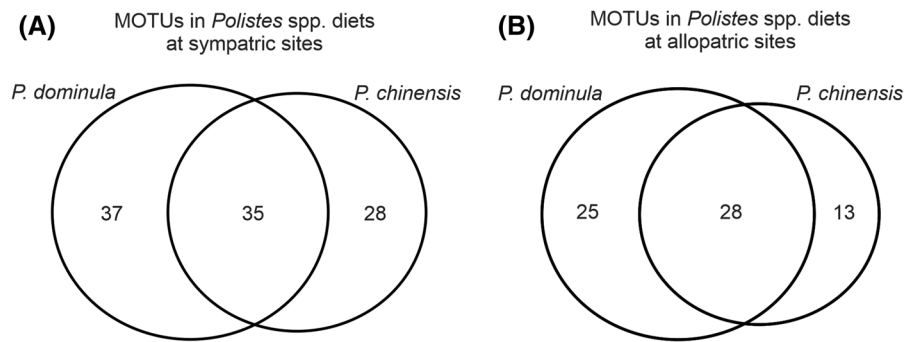


Fig. 3 Diet overlap between *P. dominula* and *P. chinensis* where they occur in sympatric and allopatric habitats. (a) In sympatric sites 100 MOTUs were identified from 29 larvae samples (15 *P. dominula*, 14 *P. chinensis*). Seventy-two (72%) of these MOTUs were found to be present in the diet of *P. dominula* and 63 (63%) were found in that of *P. chinensis*. (b)

In allopatric sites 66 MOTUs were identified from 29 larvae samples (15 *P. dominula*, 14 *P. chinensis*). Fifty-three (80%) of these MOTUs were found in *P. dominula* diet and 41 (62%) found in the diet of *P. chinensis*. Diet overlap was higher at allopatric sites but not significantly so (two-sample test of no difference in proportions: $z = 1.146$, $p\text{-value} > 0.05$)

identified as MOTUs found exclusively in *P. chinensis* samples. This would suggest that while only 46 of 123 MOTUs were found in both *P. dominula* and *P. chinensis* diets, these taxa constituted the vast majority of both species' diets. The remaining 77 taxa appear to make up a negligible proportion of *Polistes* spp. diets.

Discussion

This study suggests that when considering the presence or absence of taxa in the diets of *P. dominula* and *P. chinensis*, the two invasive wasps have different prey communities. However, quantitative assessment of the prey community reveals that overwhelmingly these wasps feed on similar prey. As generalist predators their prey are likely to be those most commonly available in a habitat, which was a mix of both native and introduced species. The overlap in diets shown here suggests that the establishment of *P. dominula* will probably negatively impact many of the same species already predated upon by *P. chinensis*. Similarly, while there are many introduced insect species present in the diet of both wasps, our estimates suggest that more than 50% of the prey DNA in the wasp diet is derived from native species.

Lepidoptera (butterflies and moths) made up the majority of prey for both species, an expected pattern based on the findings of similar analyses performed on *P. chinensis* (Ward and Ramón-Laca 2013;

Lefort et al. 2020), from the observations of *P. dominula* foraging behaviour (Stamp and Bowers 1988; Rayor et al. 2007; Baker and Potter 2020) and from diet analyses of other *Polistes* species (Kasper et al. 2004; Jeon et al. 2019). Eighty nine percent (109/123) of the taxa identified belong to the order Lepidoptera. Of these taxa, both native and introduced genera were represented. The native southern blue butterfly (*Zizina oxleyi*) was found in 57% of samples from *P. dominula* and *P. chinensis* (17/30 and 16/28 samples, respectively). This species is one of the most common butterflies in New Zealand due in part to similarly widespread host plants such as clover and other legumes (Fabaceae) (Gillespie and Wratten 2012). *Polistes dominula* has already been linked to the decline of this species and two other common butterflies in the Nelson region (McGruddy et al. 2021b). It is likely that these wasps' preference for disturbed, human-dominated habitats (Clapperton et al. 1996; Roets et al. 2019) heavily influence their diet. Native and introduced prey that also thrive in similar human-altered habitats are therefore heavily represented in their diets, as opposed to rarer species typical of more intact habitats such as forests. The spread of human influence into these more intact habitats may, however, increase the incidence of predation of native or endemic species by introduced wasps.

Another highly represented species was the light brown apple moth (*Epiphyas postvittana*), a globally important pest species (Suckling and Brockerhoff 2010). This species was found in 23% and 29%

of *P. dominula* and *P. chinensis* samples, respectively. Two other pest species were also found to make up a significant portion of *Polistes* spp. diets (Supplementary Table 2). *Polistes* spp. have been shown to exert significant predation pressure on agricultural pests, suggesting that these wasps may be ideal candidates for biocontrol (Gould and Jeanne 1984; Oliveira et al. 2017; Prezoto et al. 2019; Southon et al. 2019). These wasps have been hypothesised to be linked to the recent eradication of the invasive great white butterfly (*Pieris brassicae*) in New Zealand (Phillips et al. 2020). While we found that *Polistes* spp. prey on pest species in New Zealand we also found that 56% of the DNA retrieved from *P. dominula* samples and 52% of DNA retrieved from *P. chinensis* samples belonged to native species.

Many important herbivores were found to be present in the diet of both species. Lepidoptera, as discussed above, are important herbivores and pollinators. Hemiptera, especially cicadas (*Kikihia muta*), were shown to be significant components of *Polistes*' diets. Despite only two out of 123 MOTUs identified as taxa belonging to Hemiptera, this order was represented in 22 (73%) samples from *P. dominula* and 14 (50%) from *P. chinensis*. Hemiptera are also often important herbivores (Koch et al. 2016). The prevalence of important herbivores and pollinators in these wasps' diets may mean that sufficient numbers of either wasp species could impact not only invertebrate assemblages, but also have flow-on effects to the plant communities and the wider ecosystem. Disruption of herbivory and pollination can impact plant fitness, potentially altering the plant communities through trophic cascades. For instance, it has been shown that in the Nelson region, predation pressure exerted by *P. dominula* on monarch butterfly (*Danaus plexippus*) caterpillars was high enough to reduce herbivory on the host plant (*Gomphocarpus* sp.) to the extent that the plant's reproductive fitness was increased (McGruddy et al. 2021b). The flow-on effects produced by these invasive predators may affect more ecological communities across New Zealand as these wasps expand their range.

New Zealand's invertebrates are already facing predation pressure from invasive wasps (Harris 1991; Beggs and Rees 1999; Clapperton 1999). *Polistes chinensis* has been estimated to remove up to 957 g of prey per ha over a season from New Zealand ecosystems (Clapperton 1999). It is likely that *P. dominula*

populations could exhibit higher harvest rates than those reported for *P. chinensis* due to differences in their life history. *Polistes dominula* readily exhibits pleometrosis, a behaviour where multiple foundresses found a single colony (Höcherl and Tautz 2015; Field and Leadbeater 2016). Pleometrosis is correlated with increased colony productivity and survival (Tibbetts and Reeve 2003; Höcherl and Tautz 2015). *Polistes chinensis* is much less likely to exhibit this behaviour, with as low as 1.5% of nests containing multiple foundresses (Hoshikawa 1979). McGruddy et al. (2021a) found that nests of *P. dominula* were more productive than *P. chinensis* nests and experienced lower failure rates suggesting they could reach higher population densities. *Polistes dominula* are therefore likely to exert a higher predation pressure on New Zealand's invertebrates, presenting a greater threat to local invertebrate diversity than *P. chinensis*. The degree of diet overlap suggests that the two wasps may compete with each other for food resources.

The samples collected for this study were all from coastal locations and so the diets of both species may not represent the paper wasp diet across all of New Zealand. *Polistes dominula* has been shown to nest preferentially in human-altered habitats (Benadé et al. 2014; Roets et al. 2019). Similar work carried out in Nelson found that *P. dominula* nests translocated to sites close to human habitation and coastal sites were more productive and had higher survival rates than those in forested habitats (McGruddy et al. 2021a). The same research found no naturally occurring *Polistes* nests in surveys of forested habitat. It is therefore likely that forest species may escape most of the predation pressure by these invasive wasps. Forest species make up only 34 of the 114 butterflies and moths deemed 'at-risk' in New Zealand, with over 60% of these 'at-risk' species found in non-alpine shrubland/grasslands and coastal vegetation (Patrick and Dugdale 2000). Bioclimatic modelling has identified large areas of potentially suitable habitat for *P. dominula* across not only New Zealand but also southern Australia, southern South America and South Africa (Howse et al. 2020). In these vulnerable regions the establishment of *P. dominula* may result in similar increases in predation pressure on local insect fauna as that predicted in New Zealand.

Brock et al. (2021) describe how aculeate wasps can perform important ecosystem services as parasites, predators, biological indicators, pollinators,

decomposers and seed dispersers. It is possible that both *Polistes* spp. offer many of these benefits for biodiversity in New Zealand. For example, our analysis suggests that important agricultural pests are included in their diet. However, we estimated that more than half their prey is derived from native species. Such generalist predation behaviour has been noted as a factor that reduces the effectiveness of *Polistes* spp. as candidates for targeted pest control (Gould and Jeanne 1984; Southon et al. 2019). They are efficient predators that appear to have reduced the abundance of native butterflies and of valued species such as monarch butterflies (McGruddy et al. 2021). The threat these wasps pose to native biodiversity in New Zealand seems likely to outweigh the benefits they might provide (MacIntyre and Hellstrom 2015; Lester 2018).

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Author contributions MWFH and PJJ developed research aims and questions. MWFH wrote the draft manuscript. MWFH and RAM conducted sampling in the field and sample preparation. JB conducted laboratory work. AF and JH assisted with data analysis. All authors assisted with review and editing of the manuscript. All authors read and approved the final manuscript.

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Data and material availability Data will be made available once accepted.

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Declarations

Conflict of interest The authors declare no conflicts of interest or competing interests.

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References

- Alberdi A, Razgour O, Aizpurua O, Novella-Fernandez R, Aihartza J, Budinski I, Garin I, Ibáñez C, Izagirre E, Rebelo H (2020) DNA metabarcoding and spatial modelling link diet diversification with distribution homogeneity in European bats. *Nat Commun* 11:1–8. <https://doi.org/10.1038/s41467-020-14961-2>
- Ayesha UR, Shafi N, Akhtar T, Zareen A, Ayub H (2019) DNA barcoding of cyprinids (*Labeo rohita*, *Catla catla* and *Cirrhinus mrigala*), mitochondrial CO1-based study. *Mitochondrial DNA Part B* 4:405–407. <https://doi.org/10.1080/23802359.2018.1547132>
- Baker AM, Potter DA (2020) Invasive paper wasp turns urban pollinator gardens into ecological traps for monarch butterfly larvae. *Sci Rep* 10:9553. <https://doi.org/10.1038/s41598-020-66621-6>
- Beggs JR, Rees JS (1999) Restructuring of Lepidoptera communities by introduced *Vespula* wasps in a New Zealand beech forest. *Oecologia* 119:565–571
- Beggs JR, Brockerhoff EG, Corley JC, Kenis M, Masciocchi M, Muller F, Rome Q, Villemant C (2011) Ecological effects and management of invasive alien Vespidae. *Biocontrol* 56:505–526. <https://doi.org/10.1007/s10526-011-9389-z>
- Benadé PC, Veldtman R, Samways MJ, Roets F (2014) Rapid range expansion of the invasive wasp *Polistes dominula* (Hymenoptera: Vespidae: Polistinae) and first record of parasitoids on this species and the native *Polistes marginalis* in the Western Cape province of South Africa. *Afr Entomol* 22:220–225. <https://doi.org/10.4001/003.022.0104>
- Brock RE, Cini A, Sumner S (2021) Ecosystem services provided by aculeate wasps. *Biol Rev*. <https://doi.org/10.1111/brv.12719>
- Cameron P, Walker G, Winkler S, Hill M (2008) Interaction of a newly established immigrant, soybean looper *Thysanoplusia orichalcea* and the indigenous green looper *Chrysodeixis eriosoma* (Plutellinae: Noctuidae) in New Zealand. *N Z J Crop Hortic Sci* 36:31–39. <https://doi.org/10.1080/01140670809510218>
- Cervo R, Zacchi F, Turillazzi S (2000) *Polistes dominulus* (Hymenoptera, Vespidae) invading North America: some hypotheses for its rapid spread. *Insectes Soc* 47:155–157. <https://doi.org/10.1007/PL00001694>
- Cheng Y-C, Lin C-P (2016) Dietary niche partitioning of *Euphaea formosa* and *Matrona cyanoptera* (Odonata: Zygoptera) on the basis of DNA barcoding of larval feces. *J Insect Sci* 16:1–5. <https://doi.org/10.1093/jisesa/iew060>
- Clapperton BK (1999) Abundance of wasps and prey consumption of paper wasps (Hymenoptera, Vespidae: Polistinae) in Northland, New Zealand. *N Z J Ecol* 23:11–19

- Clapperton BK, Dymock JJ (1997) Growth and survival of colonies of the Asian paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae). *N Z J Zool* 24:9–15. <https://doi.org/10.1080/03014223.1997.9518101>
- Clapperton B, Möller H, Sandlant G (1989) Distribution of social wasps (Hymenoptera: Vespidae) in New Zealand in 1987. *N Z J Zool* 16:315–323. <https://doi.org/10.1080/03014223.1989.10422896>
- Clapperton B, Tilley J, Pierce R (1996) Distribution and abundance of the Asian paper wasp *Polistes chinensis antennalis* Perez and the Australian paper wasp *P. humilis* (Fab.) (Hymenoptera: Vespidae) in New Zealand. *N Z J Zool* 23:19–25. <https://doi.org/10.1080/03014223.1996.9518062>
- Crowder DW, Snyder WE (2010) Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. *Biol Invasions* 12:2857–2876. <https://doi.org/10.1007/s10530-010-9733-8>
- David P, Thébault E, Anneville O, Duyck PF, Chapuis E, Loeuille N (2017) Chapter one - impacts of invasive species on food webs: a review of empirical data. In: Bohan DA, Dumbrell AJ, Massol F (eds) *Networks of Invasion: A Synthesis of Concepts*. Academic Press, London, pp 1–60. <https://doi.org/10.1016/bs.aecr.2016.10.001>
- Deagle BE, Thomas AC, McInnes JC, Clarke LJ, Vesterinen EJ, Clare EL, Kartzinel TR, Eveson JP (2019) Counting with DNA in metabarcoding studies: how should we convert sequence reads to dietary data? *Mol Ecol* 28:391–406. <https://doi.org/10.1111/mec.14734>
- Eisenhauer N, Schulz W, Scheu S, Jousset A (2013) Niche dimensionality links biodiversity and invasibility of microbial communities. *Funct Ecol* 27:282–288. <https://doi.org/10.1111/j.1365-2435.2012.02060.x>
- Field J, Leadbeater E (2016) Cooperation between non-relatives in a primitively eusocial paper wasp, *Polistes dominula*. *Philos Trans R Soc b: Biol Sci* 371:20150093. <https://doi.org/10.1098/rstb.2015.0093>
- Gillespie M, Wratten SD (2012) The importance of viticultural landscape features and ecosystem service enhancement for native butterflies in New Zealand vineyards. *J Insect Conserv* 16:13–23. <https://doi.org/10.1007/s10841-011-9390-y>
- Gould WP, Jeanne RL (1984) *Polistes* wasps (Hymenoptera: Vespidae) as control agents for Lepidopterous cabbage pests. *Environ Entomol* 13:150–156. <https://doi.org/10.1093/ee/13.1.150>
- Harris RJ (1991) Diet of the wasps *Vespula vulgaris* and *V. germanica* in honeydew beech forest of the South Island, New Zealand. *N Z J Zool* 18:159–169. <https://doi.org/10.1080/03014223.1991.10757963>
- Hebert PD, Ratnasingham S, De Waard JR (2003) Barcoding animal life: cytochrome c oxidase subunit I divergences among closely related species. *Proc R Soc Lond Ser B Biol Sci* 270:S96–S99. <https://doi.org/10.1098/rsbl.2003.0025>
- Hebert PD, Penton EH, Burns JM, Janzen DH, Hallwachs W (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proc Natl Acad Sci* 101:14812–14817. <https://doi.org/10.1073/pnas.0406166101>
- Höcherl N, Tautz J (2015) Nesting behavior of the paper wasp *Polistes dominula* in central Europe—a flexible system for expanding into new areas. *Ecosphere* 6:262–262. <https://doi.org/10.1890/ES15-00254.1>
- Hoshikawa T (1979) Observations on the polygynous nests of *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae) in Japan. *Kontyu* 47:239–243. <https://doi.org/10.1080/08927014.1998.9522873>
- Howse MWF, Haywood J, Lester PJ (2020) Bioclimatic modelling identifies suitable habitat for the establishment of the invasive European paper wasp (Hymenoptera: Vespidae) across the southern hemisphere. *Insects* 11:784. <https://doi.org/10.3390/insects11110784>
- Jeon MG, Kim TG, Jung JC, Choi MB (2019) Prey diversity of *Polistes rothneyi koreanus* in different landscapes using DNA barcoding. *J Appl Entomol* 143:1052–1063. <https://doi.org/10.1111/jen.12681>
- Kasper ML, Reeson AF, Cooper SJ, Perry KD, Austin AD (2004) Assessment of prey overlap between a native (*Polistes humilis*) and an introduced (*Vespula germanica*) social wasp using morphology and phylogenetic analyses of 16S rDNA. *Mol Ecol* 13:2037–2048. <https://doi.org/10.1111/j.1365-294X.2004.02193.x>
- Koch KG, Chapman K, Louis J, Heng-Moss T, Sarath G (2016) Plant tolerance: a unique approach to control Hemipteran pests. *Front Plant Sci* 7:1–12. <https://doi.org/10.3389/fpls.2016.01363>
- Kudo K (1998) High efficiency of prey foraging achieved by frequent foraging for sawfly larvae by the foundresses of *Polistes chinensis* (Hymenoptera: Vespidae). *Entomol Sci* 1:341–345
- Kudo K (1999) Immature spiders of *Araneus abscissus*, as a prey for the pre-founding foundresses of the paper wasp, *Polistes chinensis* (Hymenoptera: Vespidae). *Entomol Sci* 2:195–196
- Lafage D, Elbrecht V, Cuff JP, Steinke D, Hambäck PA, Eriandsson A (2019) A new primer for metabarcoding of spider gut contents. *Environ DNA* 00:1–10. <https://doi.org/10.1002/edn3.62>
- Lefort M-C, Beggs JR, Glare TR, Saunders TE, Doyle EJ, Boyer S (2020) A molecular approach to study Hymenoptera diets using wasp nests. *NeoBiota*. <https://doi.org/10.3897/neobiota.63.58640>
- Lester P (2018) *The vulgar wasp: the story of a ruthless invader and ingenious predator*. Victoria University Press, Wellington
- Lester PJ, Beggs JR (2019) Invasion success and management strategies for social *Vespula* wasps. *Annu Rev Entomol* 64:51–71. <https://doi.org/10.1146/annurev-ento-011118-111812>
- Loope KJ, Baty JW, Lester PJ, Wilson Rankin EE (2019) Pathogen shifts in a honeybee predator following the arrival of the Varroa mite. *Proc R Soc B* 286:20182499. <https://doi.org/10.1098/rspb.2018.2499>
- Lyke MM, Di Fiore A, Fierer N, Madden AA, Lambert JE (2019) Metagenomic analyses reveal previously unrecognized variation in the diets of sympatric old world monkey species. *PLoS ONE* 14:e0218245. <https://doi.org/10.1371/journal.pone.0218245>

- MacIntyre P, Hellstrom J (2015) An evaluation of the costs of pest wasps (*Vespula* species) in New Zealand. Department of Conservation, Wellington
- McGruddy R, Howse MWF, Haywood J, Toft RJ, Lester PJ (2021a) Nesting ecology and colony survival of two invasive *Polistes* wasps (Hymenoptera: Vespidae) in New Zealand. *Environ Entomol* 50:1466–1473. <https://doi.org/10.1093/ee/nvab086>
- McGruddy RA, Howse MWF, Haywood J, Ward CJI, Stauffer TB, Hayek-Williams M, Toft RJ, Lester PJ (2021b) Invasive paper wasps have strong cascading effects on the host plant of monarch butterflies. *Ecol Entomol* 46:459–469. <https://doi.org/10.1111/een.12992>
- McInnes JC, Jarman SN, Lea M-A, Raymond B, Deagle BE, Phillips RA, Catry P, Stanworth A, Weimerskirch H, Kusch A, Gras M, Chereil Y, Maschette D, Alderman R (2017) DNA metabarcoding as a marine conservation and management tool: a circumpolar examination of fishery discards in the diet of threatened albatrosses. *Front Mar Sci* 4:1–22. <https://doi.org/10.3389/fmars.2017.00277>
- Ministry for Primary Industries (2016) Pest Watch. Page 26 Surveillance. New Zealand Government, Wellington
- Nakano D, Kamiya M, Tominaga O (2017) Molecular identification of macroalgal fragments in gut contents of the sea urchin *Hemicentrotus pulcherrimus*. *Fish Sci* 83:425–432. <https://doi.org/10.1007/s12562-017-1080-6>
- New TR, Samways MJ (2014) Insect conservation in the southern temperate zones: an overview. *Austral Entomol* 53:26–31. <https://doi.org/10.1111/aen.12071>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGinn D, Minchin PR, O'Hara RB, Simpson GL, Solyomos P, Stevens MHH, Szocs E, Wagner H (2019) Vegan: community ecology package. v 2.5–6. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Oliveira MM, Gomes FB, Somavilla A, Krug C (2017) *Polistes canadensis* (Linnaeus, 1758)(Vespidae: Polistinae) in the Western Amazon: a potential biological control agent. *Sociobiology* 64:477–483. <https://doi.org/10.13102/socio-biology.v64i4.1936>
- Parent CE, Peck SB, Causton CE, Roque-Albelo L, Lester PJ, Bulgarella M (2020) *Polistes versicolor* (Hymenoptera: Vespidae), an introduced wasp in the Galapagos Islands: Its life cycle and ecological impact. *Environ Entomol* 49:1480–1491. <https://doi.org/10.1093/ee/nvaa110>
- Patrick B, Dugdale JS (2000) Conservation status of the New Zealand lepidoptera. Department of Conservation, Wellington
- Paula DP, Linard B, Crampton-Platt A, Srivathsan A, Timmermans MJTN, Sujii ER, Pires CSS, Souza LM, Andow DA, Vogler AP (2016) Uncovering trophic interactions in arthropod predators through DNA shotgun-sequencing of gut contents. *PLoS ONE* 11:e0161841. <https://doi.org/10.1371/journal.pone.0161841>
- Pawson SM, Ecroyd CE, Seaton R, Shaw WB, Brouckerhoff EG (2010) New Zealand's exotic plantation forests as habitats for threatened indigenous species. *N Z J Ecol* 34:342–355
- Phillips CB, Brown K, Green C, Toft R, Walker G, Broome K (2020) Eradicating the large white butterfly from New Zealand eliminates a threat to endemic Brassicaceae. *PLoS ONE* 15:e0236791. <https://doi.org/10.1371/journal.pone.0236791>
- Pintor LM, Byers JE (2015) Do native predators benefit from non-native prey? *Ecol Lett* 18:1174–1180. <https://doi.org/10.1111/ele.12496>
- Pompanon F, Deagle BE, Symondson WOC, Brown DS, Jarman SN, Taberlet P (2012) Who is eating what: diet assessment using next generation sequencing. *Mol Ecol* 21:1931–1950. <https://doi.org/10.1111/j.1365-294x.2011.05403.x>
- Prezoto F, Maciel TT, Detoni M, Mayorquin AZ, Barbosa BC (2019) Pest control potential of social wasps in small farms and urban gardens. *Insects* 10:192. <https://doi.org/10.3390/insects10070192>
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rayor LS, Mooney LJ, Renwick JA (2007) Predatory behavior of *Polistes dominulus* wasps in response to cardenolides and glucosinolates in *Pieris napi* caterpillars. *J Chem Ecol* 33:1177–1185. <https://doi.org/10.1007/s10886-007-9283-4>
- Roets F, Benadé P, Samways M, Veldtman R (2019) Better colony performance, not natural enemy release, explains numerical dominance of the exotic *Polistes dominula* wasp over a native congener in South Africa. *Biol Invasions* 21:925–933. <https://doi.org/10.1007/s10530-018-1870-5>
- Schenk D, Bacher S (2002) Functional response of a generalist insect predator to one of its prey species in the field. *J Anim Ecol* 71:524–531. <https://doi.org/10.1046/j.1365-2656.2002.00620.x>
- Sharma H, Davies J (1983) The oriental armyworm, *Mythimna separata* (Wlk.) distribution, biology and control: a literature review. Overseas Development Administration, London
- Shaw P, Lo P, Wallis D (2001) Recent introduction and establishment of the leafroller parasitoid *Trigonospila brevifacies* (Hardy) (Diptera Tachinidae) in Nelson. *N Z Plant Prot* 54:33–36. <https://doi.org/10.30843/nzpp.2001.54.3735>
- Southon RJ, Fernandes OA, Nascimento FS, Sumner S (2019) Social wasps are effective biocontrol agents of key lepidopteran crop pests. *Proc R Soc b Biol Sci* 286:20191676. <https://doi.org/10.1098/rspb.2019.1676>
- Stamp N, Bowers M (1988) Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae). *Oecologia* 75:619–624
- Stavert JR, Pattemore DE, Bartomeus I, Gaskett AC, Beggs JR (2018) Exotic flies maintain pollination services as native pollinators decline with agricultural expansion. *J Appl Ecol* 55:1737–1746. <https://doi.org/10.1111/1365-2664.13103>
- Steinke D, Hanner R (2011) The FISH-BOL collaborators' protocol. *Mitochondrial DNA* 22:10–14. <https://doi.org/10.3109/19401736.2010.536538>
- Suckling DM, Brouckerhoff EG (2010) Invasion biology, ecology, and management of the light brown apple moth (Tortricidae). *Annu Rev Entomol* 55:285–306. <https://doi.org/10.1146/annurev-ento-112408-085311>
- Suzuki T (1978) Area, efficiency and time of foraging in *Polistes chinensis antennalis* Pérez (Hymenoptera, Vespidae). *Jpn J Ecol* 28:179–189

- Takahashi M, DiBattista JD, Jarman S, Newman SJ, Wakefield CB, Harvey ES, Bunce M (2020) Partitioning of diet between species and life history stages of sympatric and cryptic snappers (Lutjanidae) based on DNA metabarcoding. *Sci Rep* 10:1–13. <https://doi.org/10.1038/s41598-020-60779-9>
- Tibbetts EA, Reeve HK (2003) Benefits of foundress associations in the paper wasp *Polistes dominulus*: increased productivity and survival, but no assurance of fitness returns. *Behav Ecol* 14:510–514. <https://doi.org/10.1093/beheco/arg037>
- Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455–1474. [https://doi.org/10.1890/0012-9658\(1999\)080\[1455:TECOCI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1455:TECOCI]2.0.CO;2)
- Toft RJ, Rees JS (1998) Reducing predation of orb-web spiders by controlling common wasps (*Vespula vulgaris*) in a New Zealand beech forest. *Ecol Entomol* 23:90–95. <https://doi.org/10.1046/j.1365-2311.1998.00100.x>
- Turanov S, Kartavtsev YP, Lipinsky V, Zemnukhov V, Balanov A, Lee Y-H, Jeong D (2016) DNA-barcoding of perch-like fishes (Actinopterygii: Perciformes) from far-eastern seas of Russia with taxonomic remarks for some groups. *Mitochondrial DNA Part A* 27:1188–1209. <https://doi.org/10.3109/19401736.2014.945525>
- Valentini A, Pompanon F, Taberlet P (2009) DNA barcoding for ecologists. *Trends Ecol Evol* 24:110–117. <https://doi.org/10.1016/j.tree.2008.09.011>
- Vesterinen EJ, Puisto AI, Blomberg AS, Lilley TM (2018) Table for five, please: dietary partitioning in boreal bats. *Ecol Evol* 8:10914–10937. <https://doi.org/10.1002/ece3.4559>
- Ward DF, Ramón-Laca A (2013) Molecular identification of the prey range of the invasive Asian paper wasp. *Ecol Evol* 3:4408–4414. <https://doi.org/10.1002/ece3.826>
- Wilson EE, Mullen LM, Holway DA (2009) Life history plasticity magnifies the ecological effects of a social wasp invasion. *Proc Natl Acad Sci* 106:12809–12813. <https://doi.org/10.1073/pnas.0902979106>
- Wirta HK, Weingartner E, Hambäck PA, Roslin T (2015) Extensive niche overlap among the dominant arthropod predators of the high arctic. *Basic Appl Ecol* 16:86–92. <https://doi.org/10.1016/j.baae.2014.11.003>
- Zeale MRK, Butlin RK, Barker GLA, Lees DC, Jones G (2011) Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. *Mol Ecol Resour* 11:236–244. <https://doi.org/10.1111/j.1755-0998.2010.02920.x>

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