Reduced Densities of the Invasive Wasp, *Vespula vulgaris* (Hymenoptera: Vespidae), Did Not Alter the Invertebrate Community Composition of *Nothofagus* Forests in New Zealand

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ABSTRACT Invasive common wasps (*Vespula vulgaris* L.) are predators of invertebrates in *Nothofagus* forests of New Zealand. We reduced wasp densities by poisoning in three sites over three y. We predicted an increase in the number of invertebrates and a change in the community composition in sites where wasps were poisoned (wasps removed) relative to nearby sites where wasps were not poisoned (wasps maintained). Wasp densities were significantly reduced by an average of 58.9% by poisoning. Despite this reduction in wasp densities, native bush ants (*Prolasius advenus* Forel) were the only taxa that was significantly influenced by wasp removal. However, contrary to our predictions there were more ants caught in pitfall traps where wasps were maintained. We believe that the higher abundance of these ants is probably because of the scarcity of honeydew in wasp-maintained sites and compensatory foraging by ants in these areas. Otherwise, our results indicated no significant effects of reduced wasp densities on the total number of invertebrates, or the number of invertebrate families, observed in pitfall or Malaise traps. An analysis of community composition (permutational multivariate analysis of variance) also indicated no significant difference between wasp-removed or wasp-maintained communities. The most parsimonious explanation for our results is that although we significantly reduced wasp numbers, we may not have reduced numbers sufficiently or for a sufficiently long period, to see a change or recovery in the community.

KEY WORDS invasive species, native insect, invertebrate, ant, *Prolasius advenus*

Introduced or invasive animals can alter the community composition of native ecosystems by means of competition and predation (Human and Gordon 1999, Snyder and Evans 2006, Rowles and O'Dowd 2007, Bøhn et al. 2008). Predation has long been known to influence the community composition of invaded ecosystems. For example, an increase in the abundance of an invasive mantid species in the southeastern United States has reduced the abundance of other generalist predators and as a result the abundance of Hemiptera has increased (Fagan et al. 2002). Successful invasive species are also frequently superior competitors. For example, Human and Gordon (1999) found that introduced Argentine ants were able to displace native ants at resources because of a superior ability in interference competition, leading to a reduction in diversity of native species. Communities may also be structured through more complex mechanisms such as apparent competition. This structure may occur when the presence of one species indirectly decreases the

fitness of another through the presence of a shared enemy (Holt 1977, van Veen et al. 2006).

Common wasps (*Vespula vulgaris* L.) first were observed in large numbers in New Zealand in the late 1970s and have since been recorded in densities of up to 370 wasps m^{-2} of tree trunk (Moller et al. 1991). These wasps are major predators of invertebrates in *Nothofagus* forests of the South Island of New Zealand. Their high density may be driven by the abundance of honeydew from scale insects such as *Ultracoelostoma assimile* (Maskell) (Hemiptera: Margarodidae). Common wasp numbers peak between January and May and consequently numbers of other invertebrates decline as a result of strong competitive interactions and predation pressure (Moller and Tilley 1989, Beggs et al. 1998, Beggs 2001). The prey biomass consumed by common wasps has been estimated to be similar to the prey biomass consumed by the entire bird fauna, with spiders, lepidopteran larvae, and Diptera making up the majority of the common wasp diet in the early summer months (Harris 1991). The probability of orb-web spiders (*Eriophora pustulosa* Walckenaer) surviving the summer in areas where common wasps are abundant has been estimated to be effectively nil (Toft and Rees 1998). Similarly, caterpillars of the

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moth *Urisephita polygonalis maorialis* (Felder and Rogenhofer) have little chance of surviving when wasps are at their peak abundance (Beggs and Rees 1999).

The relative biomass of common wasps has been estimated to be greater than that of any other predator, introduced or native, in the *Nothofagus* forests (Thomas et al. 1990). The abundance of common wasps appears likely to have the potential to restructure both predator and prey communities. Common wasps not only impact communities through predation pressure but also have the potential to restructure communities through the mechanisms of competition (Beggs 2001, Beggs and Wardle 2006). Common wasps compete for honeydew with native insects and introduced feral honey bees (*Apis mellifera* L.). These wasps consume so much of the honeydew that it becomes uneconomical for bees to forage at times of high common wasp abundance (Moller and Tilley 1989). In both Patagonia and New Zealand invasive *Vespula* wasps can aggressively compete for food with other species, including native ants (Masciocchi et al. 2010, Grangier and Lester 2011). We note, however, that just because wasps compete with native animals in an invaded community (Masciocchi et al. 2010) and may be of relatively high abundance, their presence does not necessarily mean invertebrate communities will be significantly altered (Sackmann et al. 2008).

Because of the documented high consumption rates and low survival probabilities of native invertebrates in New Zealand honeydew beech forests (Harris 1991, Beggs and Rees 1999, Toft and Rees 1998) we predicted that a reduction in common wasp numbers would result in an increase in the number, overall diversity and community composition of native invertebrate species. We controlled ("removed") common wasp numbers through the use of toxic baits by using methods based on ongoing conservation programs run by the Department of Conservation in New Zealand. Because of similar diet and foraging patterns (Don 2007), some native ant species may be particularly impacted by common wasp competition, hence we assessed the impact of common wasp removal on the common native ant species, *Prolasius advenus* (Fr. Smith).

Materials and Methods

Study Sites. One pair of experimental sites was set up in each of three different locations in the Nelson region of the South Island of New Zealand. Each pair of sites consisted of a control site (wasps maintained) in which common wasps remained at natural levels and a treatment site (wasps removed) where common wasps were poisoned. Each site in the pair was separated by a distance of no <1.5 km, which was considered a sufficient distance as wasps have been reported to travel on average only 200 m from the nest during their foraging trips (Edwards 1980). The locations were in the Nature Recovery Area of Nelson Lakes National Park (41° 48′ S, 172° 50′ E at an altitude of 630 m, and 41° 49′ S, 172° 50′ E at 630 m), Maitai Valley east of Nelson city (41° 17′ S, 173° 21′ E at 160 m and

41° 18′ S, 173° 22′ E at 265 m), and the Roding Valley southeast of Nelson city (42° 21′ S, 173° 16′ E at 220 m and 41° 21′ S, 173° 17′ E at 270 m). At each location the vegetation was simple in structure with the canopy dominated by the mature beech trees *Nothofagus solandri* (Hook. f.) and *Nothofagus menziesii* (Hook. f.). The understory consisted primarily of *Pseudopanax* spp., *Coprosma* spp., *Cyathodes juniperina* (J.R. Forst. & G. Forst.), *Leucopogon fasciculatus* (A. Rich.), *Griselinia littoralis* Raoul, and juvenile *Nothofagus.*

Treatments and Monitoring. During February of 2008, 2009, and 2010, common wasps were poisoned at the three wasps-removed sites. This poisoning was achieved by the placement of bait stations containing Xstinguish bait (Bait Technology Ltd., Auckland, New Zealand). Xstinguish contains 0.01% fipronil, egg (protein), and sucrose (carbohydrate) (Stanley 2004). Bait stations were attached to trees in a 50- by 200-m grid pattern covering 1 km^2 surrounding each study site. Except for Nelson Lakes National Park, where because of an existing pest control program over the last 10 yr, an 8.25-km^2 area was poisoned. Any uneaten bait was removed from bait stations after 48 h, although the vast majority of the bait was consumed after this time. The effect of poisoning on wasp abundances was monitored by Malaise trapping. The mean numbers of common wasps caught in traps in both wasps-removed and wasps-maintained sites were compared between the pre- and postpoisoning periods to assess the efficacy of the wasp removal.

All six sites were sampled in December of 2007, 2008 and 2009 and January, February, and March of 2008, 2009, and 2010. This trapping regime encompassed three southern hemisphere summers. Two 20- by 20-m quadrats were established in each experimental site. Malaise traps (Townes 1972) were used to intercept flying insects. These traps consisted of a mesh tent-like structure with a collection jar at the apex, and are useful for collecting a large number of specimens. One Malaise trap was placed in the center of each quadrat. The collection jar in each Malaise trap was (1/3) filled with water with the addition of a drop of detergent to break the surface tension.

Pitfall traps are designed to opportunistically collect ground dwelling invertebrates. These traps are dug into the ground with the trap entrance flush with the soil surface. Pitfall traps were plastic cups with a diameter of 70 mm and volume of 250 ml; they were (1/3) filled with water with the addition of a drop of detergent to break the surface tension. Twenty pitfall traps were randomly placed within each quadrat no closer than two meters to any other pitfall trap.

The three locations were trapped concurrently in each of the two to four sampling dates per year for both Malaise and pitfall traps. These traps remained in place for 4 d at each site. At the end of each trapping period all traps were collected and sieved into 70% ethanol to preserve the samples. All samples were taken back to the laboratory and individuals were identified to family where possible, except for common wasps and ants which were identified to species.

Table 1. Results from the repeated measures ANCOVA examining the influence of wasp removal on the invertebrate communities

Malaise traps[a]	df	Wasps		Individuals		Families	
Source		F-value	P	F-value	P	F-value	P
Intercept	1, 39	230.473	<0.001	2720.394	<0.001	6798.596	<0.001
Location	2, 39	2.940	0.065	1.865	0.168	2.065	0.140
Time	8, 39	2.540	0.025	2.900	0.012	5.265	<0.001
Wasp removal	1, 39	12.961	0.001	0.009	0.924	0.588	0.448
Time × wasp removal	16, 39	0.086	0.967	0.281	0.839	0.849	0.475

Pitfall traps[b]	df	Ants		Individuals		Families	
Source		F-value	P	F-value	P	F-value	P
Intercept	1, 39	267.882	<0.001	1148.267	<0.001	3049.171	<0.001
Location	2, 39	8.230	0.001	0.174	0.841	0.214	0.808
Time	8, 39	2.946	0.011	6.001	0.000	2.786	0.015
Wasp removal	1, 39	5.298	0.027	0.092	0.764	0.039	0.845
Time × wasp removal	16, 39	0.683	0.568	0.533	0.662	1.221	0.315

The covariate was poisoning, which was time-dependent as it occurred during February every year and was site dependent as it occurred in the treatment sites only.

[a] Data are shown for samples taken from Malaise traps.

[b] Data are shown for samples taken from pitfall traps.

Statistical Analysis. We analyzed for differences in the numbers of wasps, ants, insects, or numbers of families of insects caught in Malaise or pitfall traps. The analyses and graphs examining the total number of insects excluded counts of the wasp *V. vulgaris,* and the ant *P. advenus,* which were each analyzed separately. The data were analyzed using repeated measures analysis of covariance (ANCOVA), with a time- and site-dependent covariate. The covariate was poisoning (coded a 0 or 1). Samples taken in wasps-maintained sites, or taken within the summer before the annual poisoning in February at wasp-removed sites, were coded as 0. Samples taken from wasp-removed sites after poisoning in March, April, or May were given the covariate code of 1. Given that the fauna at any individual site is likely to be dependent on the fauna present previously, we used a repeated measures design. As suggested by Engqvist (2005), a full model incorporating all interaction terms initially was conducted, but no significant covariate interaction terms were observed and these were removed except for the time × poison interaction. In total, 20 pitfall trap samples and two Malaise trap samples were taken at each site and each sampling date, although periodically one or two pitfall trap samples were lost because of disturbance. To avoid pseudoreplication, we averaged the samples from each site ensuring that only one "sample" was analyzed in the analysis per poisoning date and site. Data for this analysis were log10 transformed and met assumptions of normality and homoscedasticity (Levene's test of equality of error variances $P \geq 0.130$). The ANCOVA was performed in SPSS (2008).

Patterns of change in community structure before and after poisoning and between sites were assessed using abundances collected from pitfall and Malaise traps from each site. Data were analyzed in PRIMER version 6 (Clarke and Gorley 2006). Abundances contained many zero counts making parametric analysis (which assumes statistical normality) unsuitable.

Therefore, we used PERMANOVA (permutational multivariate analysis of variance) to test for differences between pre- and postsampling periods before and after common wasp poisoning. PERMANOVA uses permutation procedures to obtain *P* values, thus avoiding the usual normality assumptions of analysis of variance. Data were fourth root transformed to reduce dominance by more abundant species. The similarities percentages procedure (SIMPER) was used to calculate those taxonomic groups that contributed the most to dissimilarities between sites and sampling times. The Bray–Curtis measure of similarity was used to perform a nonmetric multidimensional scaling ordination (MDS) (Clarke and Gorley 2006).

Results

Wasp Abundances. The effect of poisoning on common wasp abundance was monitored by Malaise trapping. We observed this single annual poisoning event to significantly reduce common wasp densities in the wasps-removed sites ($P = 0.001$; Table 1a, Fig. 1a). Wasp densities varied significantly over time because of seasonal changes in their abundance ($P = 0.025$). The lack of a significant time × wasp-removal interaction indicates that the wasp densities in wasp-maintained areas were consistently higher than in wasp-removed sites throughout the study period ($P = 0.967$; Table 1a). No significant effect of site was observed, indicating similar wasp densities between different sites (Table 1).

We used to two methods to calculate the percentage reduction in wasp numbers because of the single annual poisoning event.

First, we calculated a within-year average effect of the poisoning on wasp numbers. To calculate the percentage reduction of wasp densities in wasp-removed sites, the total number of wasps observed postpoisoning in each wasp-removed site was divided by the total number observed in the paired wasp-maintained site
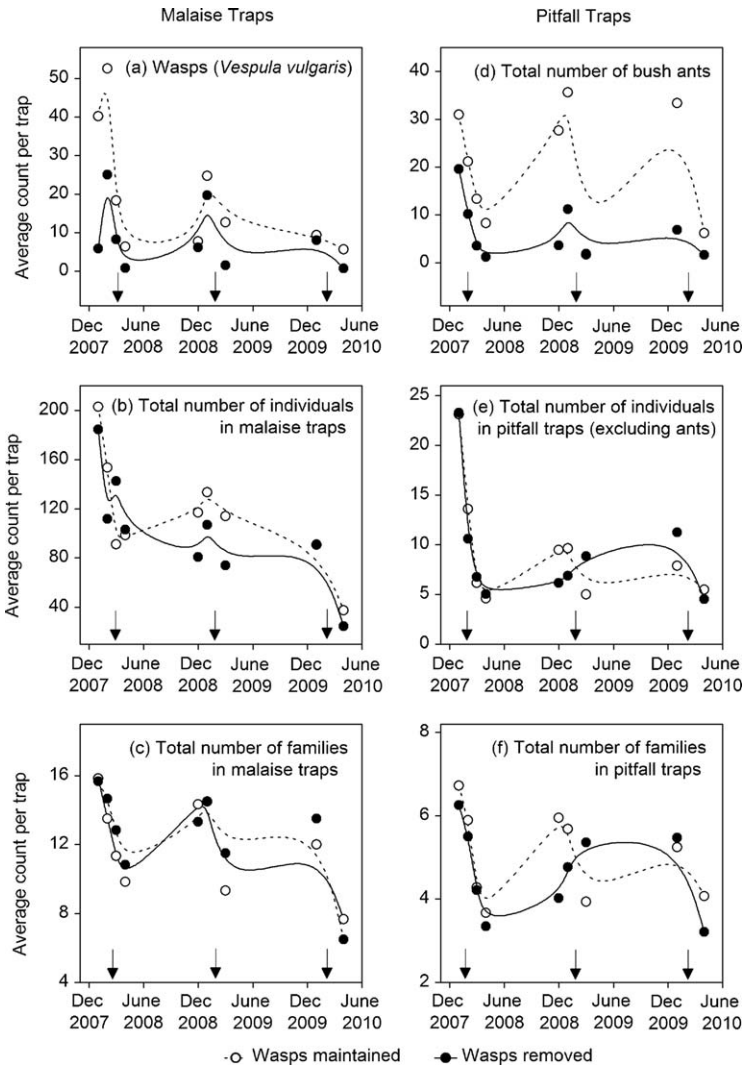
Fig. 1. The effect of wasp removal on the mean abundance of (a) common wasps (*V. vulgaris*); (b) the total number of invertebrates excluding counts of the bush ant *P. advenus*; (c) the total number of families, in Malaise traps, and in pitfall traps; the (d) total number of the bush ant *P. advenus*; (e) the total number of individuals; and (f) the number of families. Arrows indicate the dates of poisoning, although the poisoning was conducted in only wasps-removed sites. Lines are spline curves. Each point represents the average of the density from each of the three sites.

over the corresponding spring–autumn sampling period. This calculation gave an average annual reduction of wasp densities of $52.8 \pm 10.8\%$ (mean $\pm$ SE, $n = 3$ yr) for the Lakehead site, $89.5 \pm 8.4\%$ for Roding, and $96.5 \pm 1.8\%$ for Maitai.

Second, we calculated an overall effect of the wasp control program for each of the three sites over the 3-yr period of this study. We thus divided the total number of wasps observed in the wasp-removed sites (counted from after the first poisoning event in 2008 until the last sample in 2010) by the wasp-maintained site over the corresponding period. This calculation gave an overall annual reduction of wasp densities of 19.3% for the Lakehead site, 66.9% for Roding, and 90.5% for Maitai. The result indicating the site with

the lowest overall control (Lakehead) was largely because of recovery of wasp populations in the summer of 2009 before the annual poisoning event within the same year. In this site during 2009, before the annual poisoning event 106 wasps were observed in wasp-removed site samples compared with 107 in the in wasp-maintained site. The average overall effect of wasp removal for all sites was thus $58.9 \pm 20.9\%$. This estimate of control is thus substantially less than observed in the estimate of the annual reduction.

Invertebrate Community Composition: Malaise traps. In total, there were 12,925 individuals from 44 families or taxonomic groups present in Malaise traps over the three trapping seasons (Fig. 1b and c).

In our analysis on the number of individuals caught in Malaise traps we observed no significant effect of wasp removal ($P = 0.924$; Table 1a, Fig. 1b). The ANCOVA indicated that there was a significant effect of time, indicating a significantly varying catch of invertebrates across different sampling times ($P = 0.012$; Table 1a, Fig. 1b). Similarly, there were no significant effects of location nor a significant time × wasp removal effect on the number of individuals caught in the Malaise traps (Table 1a, Fig. 1b).

The analysis of families similarly indicated no significant effect of wasp removal ($P = 0.448$; Table 1a, Fig. 1c). There was a significant change in the numbers of families caught in malaise traps over the duration of the study, with the peak abundance occurring in mid-summer and declining in autumn (Table 1a, Fig. 1c).

PERMANOVA revealed that the composition of invertebrate communities caught in Malaise traps was not significantly different between wasp-maintained and wasp-removed sites (Pseudo $F = 0.691$; df = 1,8; $P = 0.756$), which also was reflected in the MSD plots (Fig. 2a). Significant differences in composition were observed between sampling periods (Pseudo $F = 7.847$; df = 1,8; $P < 0.050$), but there was no difference between locations (Pseudo $F = 0.887$; df = 2,9; $P = 0.524$). In addition, there was no time × wasp-removal interaction between treatment and time, indicating that the observed differences are because of seasonal differences in community composition (Pseudo $F = 0.750$; df = 1,8; $P = 0.678$). SIMPER analysis determined that plots were 28% dissimilar between sampling periods in Malaise traps. Of this variation, 30% was explained by five taxonomic groups: Trichoptera, Mordellidae, Empididae, Pompilidae, and Hemiptera. Trichoptera were three times more abundant in the prepoisoning period and Pompilidae were twice as abundant before poisoning.

Invertebrate Community Composition: Pitfall Traps. In total, there were 34,892 individuals from 44 families caught in pitfall traps over the three trapping years (Fig. 1e).

Reducing wasp densities by poisoning did not significantly increase the number of invertebrates caught in pitfall traps ($P = 0.764$; Fig. 1e). Numbers of invertebrates changed significantly over time, but did not vary significantly between locations (Table 1b). The time × wasp-removal interaction effect was also not significant (Table 1b).

Reducing wasp densities by poisoning also did not significantly change the mean number of taxonomic groups, or families, caught in pitfall traps ($P = 0.845$; Fig. 1f). The ANCOVA indicated a significant effect of time, but no effect of location or time × wasp-removal interaction (Table 1b).

The PERMANOVA similarly indicated no significant difference in the community composition caught in pitfall traps between wasp-maintained and wasp-removed sites (Pseudo $F = 0.956$; df = 1,8; $P = 0.492$) or between locations (Pseudo $F = 1.661$; df = 2,8; $P = 0.067$) (Fig. 2b). In accordance with the ANCOVA results, a significant effect of time was observed in the PEMANOVA (Pseudo $F = 4.026$; df = 1,8; $P < 0.010$),
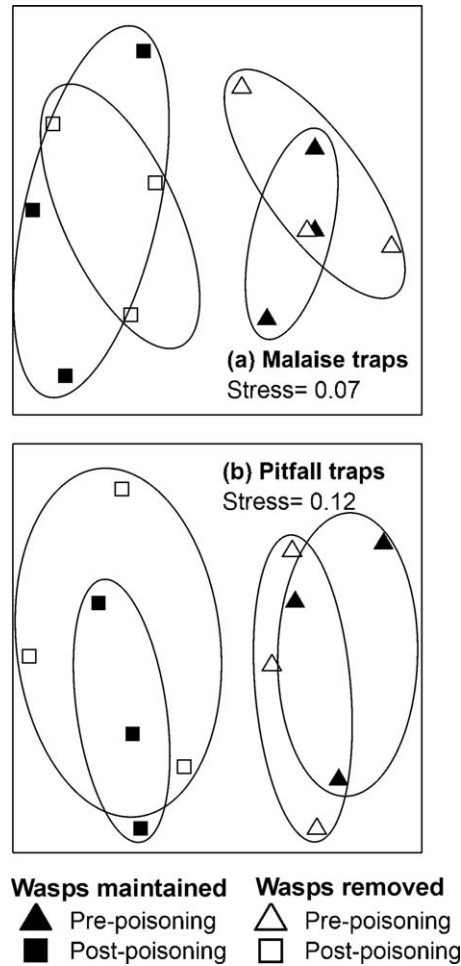

(a) Malaise traps
Stress= 0.07

(b) Pitfall traps
Stress= 0.12

Wasps maintained
▲ Pre-poisoning
■ Post-poisoning

Wasps removed
△ Pre-poisoning
□ Post-poisoning

Fig. 2. Multidimensional scaling (MDS) plots from arthropod communities caught in (a) malaise traps, and (b) pitfall traps. Samples were taken before and after common wasp poisoning in wasps-removed and wasps-maintained sites. Wasps-removed sites had wasp poison placed and wasp density was reduced by an average of 58.9% (±14.0). Wasps-maintained sites were not poisoned and common wasps remained at natural levels. Data were collected over 3 yr. Each point represents pooled data from one sampling site.

but no time × wasp-removal interaction (Pseudo $F = 0.501$; df = 1,8; $P = 0.867$). The stress value of 0.12 in the MDS plot indicates that the plot configuration is close to actual dissimilarities (Fig. 2b). SIMPER analysis of pitfall traps determined that plots were 26% dissimilar between sampling periods. Of this variation, 30% was explained by seven taxonomic groups: ants, Histeridae, Staphylinidae, Calliphoridae, Lygaeidae, Psychodidae, and Margarodidae. Ants were twice as abundant in the prepoisoning period and Histeridae were almost three times more abundant before poisoning.

Ant Abundances. Ants were extremely abundant in the pitfall traps. The total number of ants observed in these traps frequently exceeded the total number of all other invertebrates caught (Fig. 1d, e). These ants

were almost all *Prolasius advenus* (Forel). The average abundance of *P. advenus* in the pre- and postpoisoning periods was 48.18 (±13.11) and 5.01 (±1.15), respectively. In comparison, the numbers of the second most abundant ant species, *Huberia brounii* (Forel), caught in pitfall traps were very low (0.18 ± 0.02, and 0.11 ± 0.04 per trap, in the pre- and postpoisoning periods, respectively).

Contrary to our expectations, the numbers of *P. advenus* caught in pitfall traps were significantly higher in wasp-maintained than in wasp-removed sites (*P* = 0.027; Fig. 1f). In addition, there were significant effects of time and location on *P. advenus* abundance (*P* ≤ 0.011), although the time × wasp-removal interaction was not significant (*P* = 0.568; Table 1b).

Discussion

Previous work has shown that common wasps can reduce both invertebrate abundance and the diversity of the invertebrate community (Harris 1991, Moller et al. 1991, Beggs et al. 1998, Beggs 2001). We predicted that a reduction in common wasp numbers would result in an increase in the number, overall diversity, and community composition of native invertebrate species. Although we significantly reduced common wasp abundances, no significant effects were observed on the invertebrate communities. We did observe significant seasonal variation in the abundance within the invertebrate community composition, although this variation likely reflects the biology of various community members. For example, the Trichoptera caught in Malaise traps were three times more abundant at the start of the summer than at the end. This variation is a natural phenomenon, as peak summer emergence for Trichoptera in New Zealand is between December and January (Collier and Smith 1998). The only species to show a significant response to wasp removal was the ant *P. advenus.*

There are several hypotheses to explain our findings. 1) There may be no effect of common wasps on the invertebrate community; 2) communities take much longer to recover from invasion than we were able to detect in the short period of our study; 3) we may not have reduced common wasp numbers sufficiently to see an effect, or there was too much variation in wasp control between sites; 4) we may have conducted the poisoning treatment too late in the season; and 5) we may have missed variation by only identifying samples to the family level. We will address each of these potential explanations in turn.

It is conceivable that common wasps may have no effect on the community composition of invertebrates in this system. We note that a study similar to ours also found no significant change in the invertebrate community as a result of *Vespula germanica* (F.) control in northwest Patagonia, although in that community wasp densities were much lower than those that we observed (Sackmann et al. 2008). However, this explanation seems unlikely in the light of numerous other studies that document an impact of common wasps on native invertebrates in New Zealand

Nothofagus forests (Harris 1991, Toft and Beggs 1995, Toft and Rees 1998, Beggs and Rees 1999, Beggs 2001). It is possible that species that are particularly vulnerable to common wasp predation may have already become scarce in areas with high common wasp abundance such as these *Nothofagus* forests, and the limited period of our experiment (only 3 yr) may not be of a sufficiently long time frame to see any recovery in the natural community. This invertebrate community has been subject to invasion by the wasp *Vespula germanica* since the 1940s and common wasps since the 1980s (Toft and Rees 1998). For the community to be able to recover from these *Vespula* spp. invasions it may take considerably longer than 3 yr of wasp removal.

We may not have reduced common wasp numbers sufficiently to see a recovery in the community. It is possible that only those species less impacted by common wasps remain in these communities. To be able to detect any recovery in vulnerable species, common wasp numbers may need to be reduced to a greater extent. Even if the poisoning effort were to continue long–term, as is the case at Lakehead where there is an existing predator control program where common wasps have been poisoned for the last 10 yr, the within-in-season average reduction in common wasp numbers by only 52.8% may not be enough to have a significant impact on the abundance and diversity of prey species. The other two sites had higher levels of wasp control, but the variation between sites may have limited our ability to show a significant result. It has been estimated that to conserve species vulnerable to common wasp predation, common wasp numbers need to be reduced by 80–90% (Beggs et al. 1998, Toft and Rees 1998, Beggs and Rees 1999). Baits and protocols for such a high level of efficacy with *Vespula* wasps (Hanna et al. 2012), though, require a relatively high intensity and effort. The New Zealand Department of Conservation may need to consider such a poisoning protocol if invertebrate conservation and community recovery are a priority, rather than using the existing protocol which we replicated in this study. Of particular interest to conservation authorities was the apparent variation in the effects of the same poisoning treatment between the three study sites. The effect of the poisoning on wasp densities over the duration of the study varied from 19.3 to 90.5%. We are unsure of reasons for this variation, but clearly implementing a standard management plan to effectively control wasps in all sites is very difficult. The variation in wasp control across sites possibly contributed to the lack of significant effects in this study.

It is also possible that we may have conducted the poisoning treatment too late in each season to see an impact of a reduction in common wasp numbers on the invertebrate community. The life-history stage that is most susceptible to wasp invasion for many invertebrates is likely to be when they are in the larval stage, which for many invertebrates is early in the season before wasp poisoning. Poisoning took place at the point of highest common wasp abundance, in our study at the end of February. This method was used as

studies have shown that poisoning before this time is ineffective, as there is often such an abundance of other prey species that common wasps are not attracted to protein bait (Beggs et al. 1998, Beggs 2001). The impact of high common wasp numbers before poisoning may thus have reduced the numbers of prey for the remainder of the summer.

In addition, our method of identifying invertebrates only to family may have missed variation in the community as a result of common wasp removal. If we had identified our catch to species, or even genus, we may have picked up changes based on preferential predation from common wasps. However, given the time and logistical constraints of species identification it was decided a priori that the family level of classification would be sufficient.

The numbers of the ant *P. advenus* declined in pitfall traps as a result of the annual poisoning event. Our initial observations of this decline led us to suspect that the toxic bait may have nontarget effects on these ants, especially because these native ants compete aggressively for protein with common wasps (Grangier and Lester 2011). We subsequently spent considerable time observing the toxic-bait stations, which are nailed to trees ≈1 m from the ground. No ants ever were observed foraging on these stations during the night or the day. Rather than nontarget effects, recent work in laboratory experiments suggest that decrease in ants caught in pitfall traps may be because of a change in their foraging behavior. In these experiments we connected nest boxes of *P. advenus* to experimental foraging arenas. When deprived of carbohydrates for 6 mo, we observed an ≈10-fold increase in the number of *P. advenus* workers foraging in these arenas relative to control treatments (Grangier and Lester, in preparation). Wasps are known to be highly efficient foragers and deplete carbohydrates in forest ecosystems (Moller and Tilley 1989) and may alter their foraging patterns or behavior according to resource availability (Mailleux et al. 2003, Grover et al. 2007). We suspect that the significantly higher number of ants caught in our wasp-maintained relative to wasp-removed sites, probably represents a similar increase in foraging behavior as a result of carbohydrate deprivation.

We cannot exclude the possibility that wasps are not having an effect in these communities and are thus not a universally "bad" invasive species. Others also have not observed significant impacts of *Vespula* spp. invasions from wasp-removal studies (Sackmann et al. 2008).We believe, however, that the most parsimonious explanation for the lack of effects on the invertebrate community as a result of wasp removal was that we did not reduce common wasp numbers sufficiently, that the variation between replicate study sites in response to poisoning resulted in a lack of statistical significance, or both. This result would be in agreement with other researchers whom have suggested that wasp abundances need to be reduced by 80–90% to conserve species vulnerable to common wasp predation (Beggs et al. 1998, Toft and Rees 1998, Beggs and Rees 1999). Further, it may take many years of such a reduced wasp density to more robustly determine the community effects of common wasp removal. Even under these conditions, species that are particularly vulnerable to common wasp predation or competition may have already been permanently excluded from this system.

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