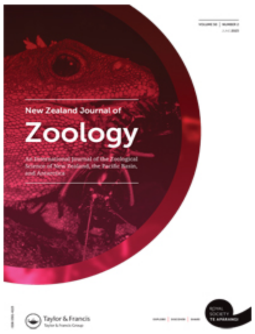

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RESEARCH ARTICLE

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Changing distributions of the cosmopolitan mosquito species *Culex quinquefasciatus* Say and endemic *Cx. pervigilans* Bergroth (Diptera: Culicidae) in New Zealand

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ABSTRACT

New Zealand has 13 endemic mosquito species, which are predominantly bird-biters, exhibiting low levels of vector competence, and are adapted to their native ecosystems. Anthropogenic land-use change are well-suited to domesticated exotic species that have already established here. While some endemic species, such as *Culex pervigilans,* can also be found vutilising such environments, there are indications of population decline and displacement. The cosmopolitan *Cx. quinquefasciatus* has been established in New Zealand for more than 180 years, and was believed to be confined to the warmer, northern regions. However, biosecurity records of obtained specimens collected by the National Mosquito Surveillance Program, at various points of entry (POE) for goods and international travel, suggest an expansion of this range. Changes in the distributions of *Cx. quinquefasciatus* and *Cx. pervigilans* over the last fifteen years in New Zealand, are evaluated herein, with the conclusion that *Cx. quinquefasciatus* is increasing both in distribution and population density over time, and should be considered an invasive species. Evidence of a southward spread is likely a result of anthropogenic environmental changes particularly favourable to *Cx. quinquefasciatus.* A trend of considerable ecological and public health importance. Similarly clear effects on urban *Cx. pervigilans* populations were not observed.

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Introduction

Global travel and trade are spreading some mosquito species beyond their natural and historic ranges. This raises concerns regarding the spread of competent disease-vector species and pathogens of public health importance (Weinstein et al. 1997; Lounibos 2002). Furthermore, it has been shown that increasing numbers of international flights and shipping arrivals result in more frequent interceptions of exotic mosquito species

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(Gratz et al. 2000; Tatem et al. 2006). These are typically transported by sea as larvae, often in used-machinery and tyres; or as adults, by air (Ammar et al. 2019). Continued interceptions of exotic mosquito species, considered in combination with climatic and environmental changes, suggest an increased likelihood of establishment and adaptation to new environments (Semenza and Suk 2017). Further local dispersal then occurs mostly via road vehicles (Medlock et al. 2012).

The success of a mosquito species in colonising new geographic locations may depend on its ability to adapt to novel climatic and environmental conditions. This may include, for example, the respective seasonalities of both source and arrival locations, or facultative production of cold or desiccation resistant eggs in temperate or drought prone regions. Artificial water containers (e.g. used tyres, sumps, roof gutters, discarded packaging) in rural and built environments provide larval habitats for more domesticated species; and by extension, opportunities for human exposure to nuisance biting and potential pathogen transmission.

Culex quinquefasciatus Say, 1823 is one of the most widespread mosquitoes globally between the latitudes 36° N and 36° S (Samy et al. 2016). It is a competent vector overseas of *Wuchereria bancrofti* (Cobbold, 1877) (cause of filariasis) (Belkin 1968), and Japanese encephalitis virus (Reuben et al. 1994). In the northern hemisphere it is a vector of West Nile virus (Goddard et al. 2002; WHO 2017) in humans. There appear to be regional differences in vector competence of this species which range from some populations which are very poor vectors in nature, to those that are good vectors with excellent transmitting capabilities (Sardelis et al. 2001).

For instance, there has been little evidence of vector competency in *Cx. quinquefasciatus* for dengue (Vazeille-Falcoz et al. 1999) or for Murray Valley encephalitis, Kunjin, and Ross River viruses (Kay et al. 1982) in the lab. However, other studies show a link of high abundancy of *Cx. quinquefasciatus* in a dengue transmission hotspot, especially if co-abundant with a strong vector (e.g. *Aedes aegypti*) (Ka-Chon Ng et al. 2018).

In New Zealand to date, the species has been implicated in transmission of avian pox virus (Castro et al. 2011) and the avian malaria-causing protozoa (Derraik 2004; Derraik and Slaney 2005), *Plasmodium relictum* Grassi & Feletti, 1891 (Laird 1996) and *P. cathemerium* (Hartman, 1927) (Lee et al. 1989; Schoener et al. 2014).

While occurring in a range of environments, *Cx. quinquefasciatus* usually breeds alongside other local species in organically rich and polluted surface waters or artificial containers (Lee et al. 1989; Weinstein et al. 1997), which brings the species in close contact with human activities. The adults remain relatively close to their breeding habitat and host sources, within a flight range of approximately one kilometre (Schreiber et al. 1988; Reisen et al. 1991). When breeding, Australian *Cx. quinquefasciatus* are known to swarm in large numbers (Lee et al. 1989) and are considered bird-biters. However, there is a seasonal spillover of biting activity to other wildlife, livestock, and humans (Holder et al. 1999; Malkinson and Banet 2002; McLean et al. 2002). As nocturnal-biters the females readily venture indoors (Weinstein et al. 1997). This species is called the 'Southern House Mosquito' in the USA, where it is probably more adapted to urban habitat than in New Zealand.

In Aotearoa, *Cx. quinquefasciatus* is now also one of the most common mosquitoes and, together with *Aedes notoscriptus* (Skuse, 1889), is reported as a nuisance for humans (MOH 1998). It is believed to have been first introduced in the 1830s (Sandlant

2002), probably carried by American whaling ships (Weinstein et al. 1997), or as larvae in open water storage tanks on vessels from Australia entering ports at the Bay of Islands and Auckland (Laird 1990).

The species range was initially restricted to areas around points of entry (POE) for international travel and freight, but this range has, over time, expanded inland and southward (Laird 1995; Weinstein et al. 1997; Holder et al. 1999).

Cx. quinquefasciatus was known from the North Island and northern parts of the South Island including Marlborough, Picton and Nelson (Weinstein et al. 1997). It has occasionally been detected in traps in Christchurch and Queenstown; however, it does not appear to have established in either area, possibly due to longer and colder winters (M. Disbury pers. comm.) but is now found more frequently in Christchurch (NZB-Border Health Newsletter; Figure 1).

Cx. pervigilans Bergroth, 1889 is the most common and widespread endemic mosquito species in New Zealand (Belkin 1968; Holder et al. 1999). Evolving alongside birds in the absence of mammals, *Cx. pervigilans* is, as are most New Zealand mosquito species, considered as a bird biter, although it seems to be adapting to new blood meal opportunities such as mammals including humans and cattle (Holder et al. 1999; Derraik and Slaney 2005). Like *Cx. quinquefasciatus*, it may be a vector for avian malaria (Holder et al. 1999; Schoener et al. 2014) and has been implicated in the spread of avian pox virus (Alley MR et al. 2010).

Because of its ability to utilize a wide variety of breeding habitats, including artificial containers, *Cx. pervigilans* can be abundant in both rural and built environments (Derraik and Slaney 2005). It has been found throughout the North and South Islands, Chatham Island, Auckland Islands and also the Kermadec Islands (Belkin 1968; Dumbleton 1968; Sandlant 2002).

In order to compare the abundance and distribution over time of these two *Culex* species, one introduced, one endemic, we have analysed the National Surveillance records from 2005–2020 and specifically addressed the following questions for urban areas:

1. Have mosquitoes in New Zealand, increased in general over the last 15 years or is *Cx. quinquefasciatus* increasing independently?
2. Is *Cx. quinquefasciatus* spreading geographically across the country?
3. Is *Cx. quinquefasciatus* increasing in particular localities in New Zealand and is there any trend evident for *Cx. pervigilans*?

Material and methods

Data

Occurrence data for *Culex quinquefasciatus* and *Cx. pervigilans* were obtained from the Online National Mosquito Surveillance database. This contains all mosquito sampling results from the National Mosquito Surveillance programme undertaken for the Ministry of Health (MOH) and maintained by NZ BioSecure 2005–2020.

Health protection officers from 12 District Health Boards (DHBs) nationwide (Figure 1A) routinely monitor mosquitoes at and around international sea and air ports that are considered POEs. While the focus for this is early detection of unwanted species, local resident species are included and this provides a basis to consider current trends and future projections for these species. Surveillance methods include larval and adult trapping as well as sampling of on-site waterbodies in accordance with the

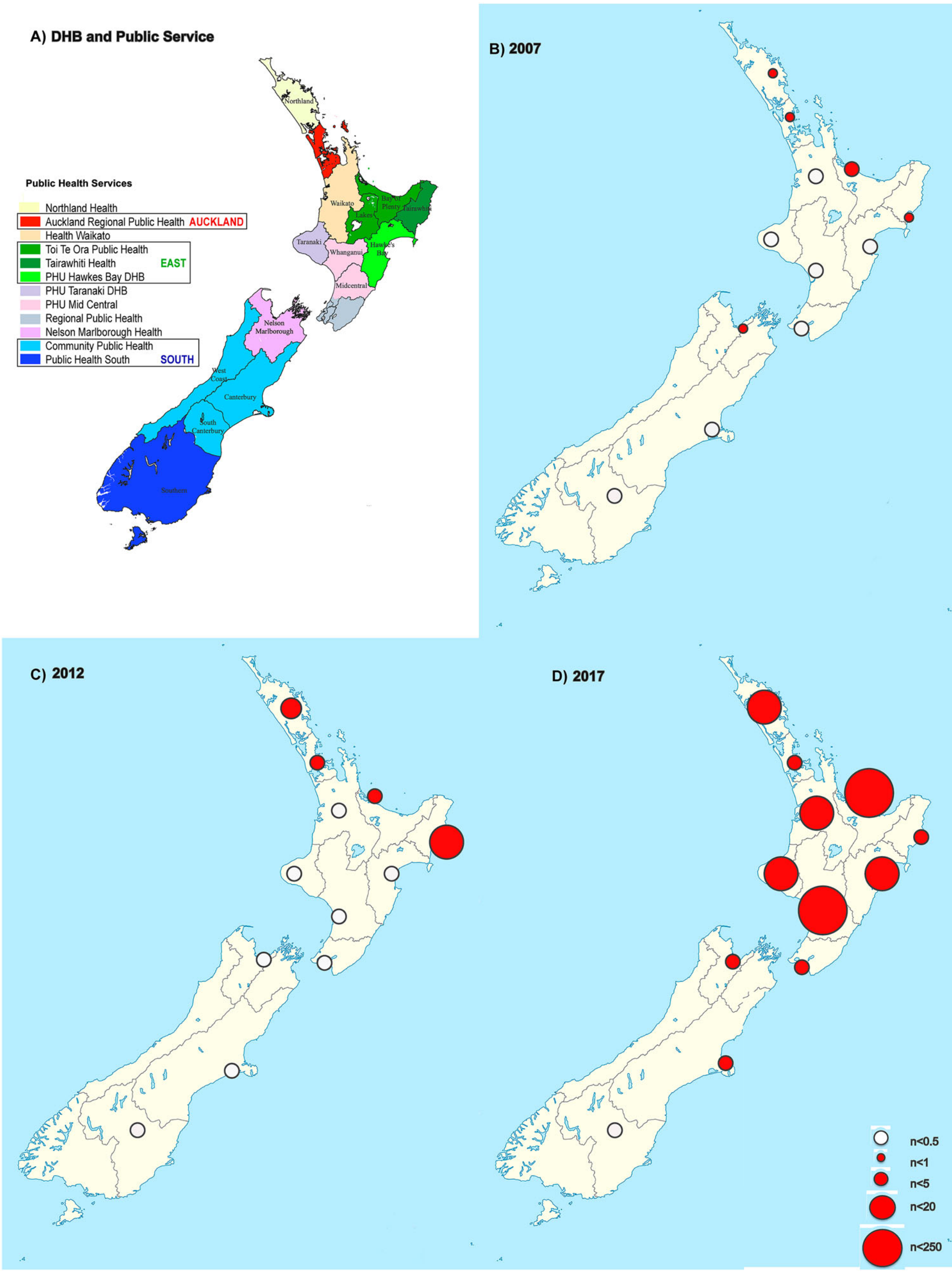

Figure 1. A, Map of the district health boards, with outlined NZ DHB areas highlighting the three areas of interest: Auckland, East and South. **B,** 2007; **C,** 2012; **D,** 2017 showing the mean catch-rate of the invasive mosquito species *Culex quinquefasciatus* during the mosquito surveillance.

standardised trapping and sampling procedures outlined in NZ BioSecure 2019 (see also International Health Regulations CDC 2013, 2017; WHO 2016; and references therein).

Identifications are confirmed by taxonomists at the New Zealand BioSecure Entomology Laboratory (Lower Hutt) and survey details recorded in the Online National Mosquito Database. All records 2005–2020 were evaluated as follows.

Per year, each sample was classified by locality (regional DHB) (Supplementary material) and as positive or negative for mosquitoes, then positive samples with *Cx. pervigilans* and/or *Cx. quinquefasciatus* were identified as adult or larval samples. Thus, for each combination of year, location, species (*Cx. quinquefasciatus* or *Cx. pervigilans*) and life stage (larvae or adult), we obtained a value for the number of positive samples (containing mosquitoes) and the total number of specimens collected (see supplemental table Table S1).

Statistical analyses

For the purpose of statistical analysis, the mosquito surveillance data from all 12 DHB areas were initially examined; from which, three aggregate areas of particular interest were selected, and examined individually. These were Auckland region (referred to as 'Auckland'), which includes many major international POEs for travel and freight, and represents a large proportion of national surveillance efforts; the ports of Tauranga, Gisborne and Napier as key POEs for freight (referred to jointly as 'East'); and the areas of Canterbury and Southern DHBs (referred to as 'South') as a wider area with occasional records and potential for spread of *Culex quinquefasciatus*. This excluded central samples (Wellington, mid Central, Taranaki, Nelson and Waikato DHBs).

All analyses were performed in R version 4.0.2 (R core team 2020). All tests described below were performed separately for records of adult and larval specimens.

Firstly, the presence of mosquitoes in general, relative to sampling effort was examined over the period 2005–2020. For this a generalised linear model with binominal error

Table 1.

a) Proportion of positive mosquito samples						
Area	**Life stage**	**Term**	**n**	**df**	**χ2**	**p-value**
All locations	larvae	location: year	192	11	923.70	**< 0.01**
All locations	adults	location: year	192	11	426.93	**< 0.01**
Clustered	larvae	location: year	96	2	37.99	**< 0.01**
Clustered	adults	location: year	96	2	235.05	**< 0.01**
b) Proportion of samples positive for *Cx pervigilans* & *Cx quinquefasciatus*						
Area	**Life stage**	**Term**	**n**	**df**	**χ2**	**p-value**
Clustered	larvae	location : year : species	192	2	321.08	**< 0.01**
Clustered	adults	location : year : species	192	2	49.64	**< 0.01**
c) Total number of mosquitos						
Area	**Life stage**	**Term**	**n**	**df**	**χ2**	**p-value**
Clustered	larvae	location : year : species	192	2	28.1	**< 0.01**
Clustered	adult	location : year : species	167	2	1.38	0.50
		year : species	167	2	0.00	0.98
		location : year	167	2	2.25	0.33
		location : species	167	2	6.80	**0.03**
		year	167	1	11.66	**< 0.01**

structure and logit link function was used to test whether year and capture location were associated with the proportion of positive samples (adults or larvae present). Two-way interaction between these variables was also explored. All 12 DHB regions were examined initially then the analysis was repeated for the three aggregate areas of 'Auckland', 'East' and 'South' as regions of special interest.

Next, and using only positive samples with similar procedures, the occurrence of *Cx. pervigilans* and *Cx. quinquefasciatus* was each examined relative to other mosquitoes using year, capture location and species as test variables and also including three-way and respective two-way interactions.

Finally, changes over time (by year per season, i.e. July to June) in the specimen counts of each target species relative to sampling effort (numbers of samples collected) was examined for the 'Auckland', 'East' and 'South' areas. For this a generalised linear model with quasi-Poisson error structure and log link function was used to test whether mosquito counts per sample, adjusted for numbers of samples collected in each region, showed any year to year trend, and whether this differed between these regions. Therefore, capture location and species were used as explanatory variables with the three-way interaction between year, location and species and respective two-way interactions.

Results

General sampling success for all mosquitoes (proportion of positive samples)

In all cases there was a significant influence of date and location on the occurrence of both larvae and adults (Table 1), reflected in the total number of positive samples for both life stages.

The sample-success rate for larvae in Northland, Midcentral and Gisborne (Figure 2A) was generally high across the analysed period (proportions 0.4–0.7) but variable between years; with all three of these regions trending downward over time, most notably in Gisborne. A similar downward trend was seen in Taranaki and Nelson, and the inverse (a slight upward trend) in Auckland, Waikato, Wellington and Hawkes Bay. Sampling success for Tauranga, Canterbury and the Southern Districts remained stable (Figure 2A).

There was greater variation apparent in the adult sampling-success rates, where the Auckland, Waikato, Hawkes Bay, Wellington, Canterbury and far-South demonstrated a slight downward trend, contrary to the larvae trend in these regions. This was most pronounced in Northland where a clear increase in adult sample-success juxtaposed the decrease in larvae sample-success (Figure 2B).

Merging the regions of particular interest into clusters: Auckland, East and South, the sampling success of mosquito larvae was somewhat stabilised over the 15-year period; though in aggregate, the catch rates for all adults went down (South exhibiting the sharpest decline). A decrease in variability of sample-success could be seen in the individual localities over time, and in the merged localities over the last five years (Figure 3A and B).

Sampling success for **Culex pervigilans** *and* **Cx. quinquefasciatus** *(proportion of positive samples)*

There was a significant influence of year and location and a difference between species for adults and larvae in the proportions of positive samples for both *Cx. pervigilans* and *Cx.*

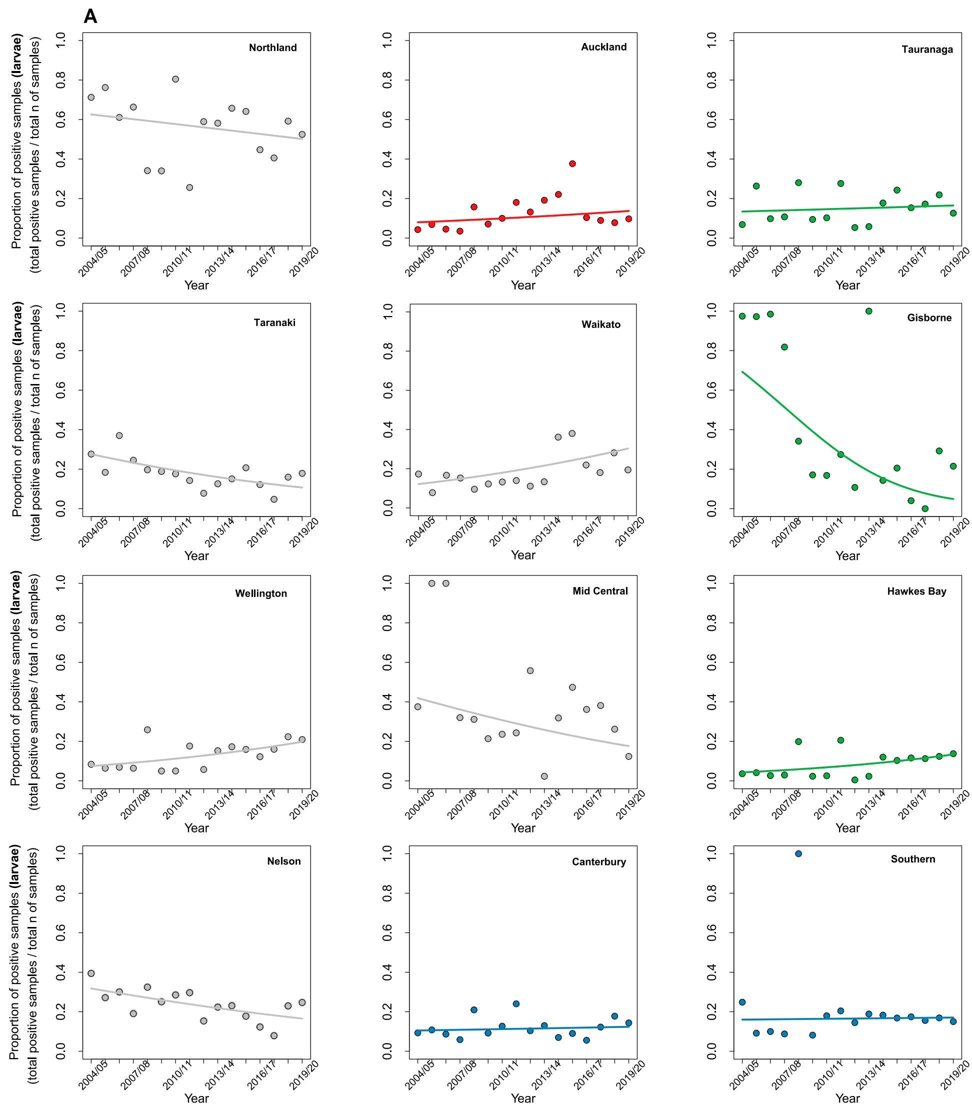

Figure 2. Proportion of samples positive for mosquitoes according to sampling effort by DHB locations location between 2012 and 2020: **A,** for larvae; **B,** adults (red, Auckland; green, East; blue, South)

quinquefasciatus (Table 1). Overall *Cx. pervigilans* clearly presented as the dominant species in the South cluster for both larvae and adult, with far greater positive sample rates than those seen in the Auckland and East clusters.

Catch rates for *Cx. pervigilans* larvae and adults remained relatively low but consistent in both the East and Auckland clusters; although a small increase over time in sample success rate was evident in Auckland (Figure 4A and C).

There were few or no positive samples of *Cx. quinquefasciatus* larvae or adults in the South cluster before 2015–16 but there has been a clear increase for both larval and adult samples in the years since. (Figure 4B and D). This species was already active in the

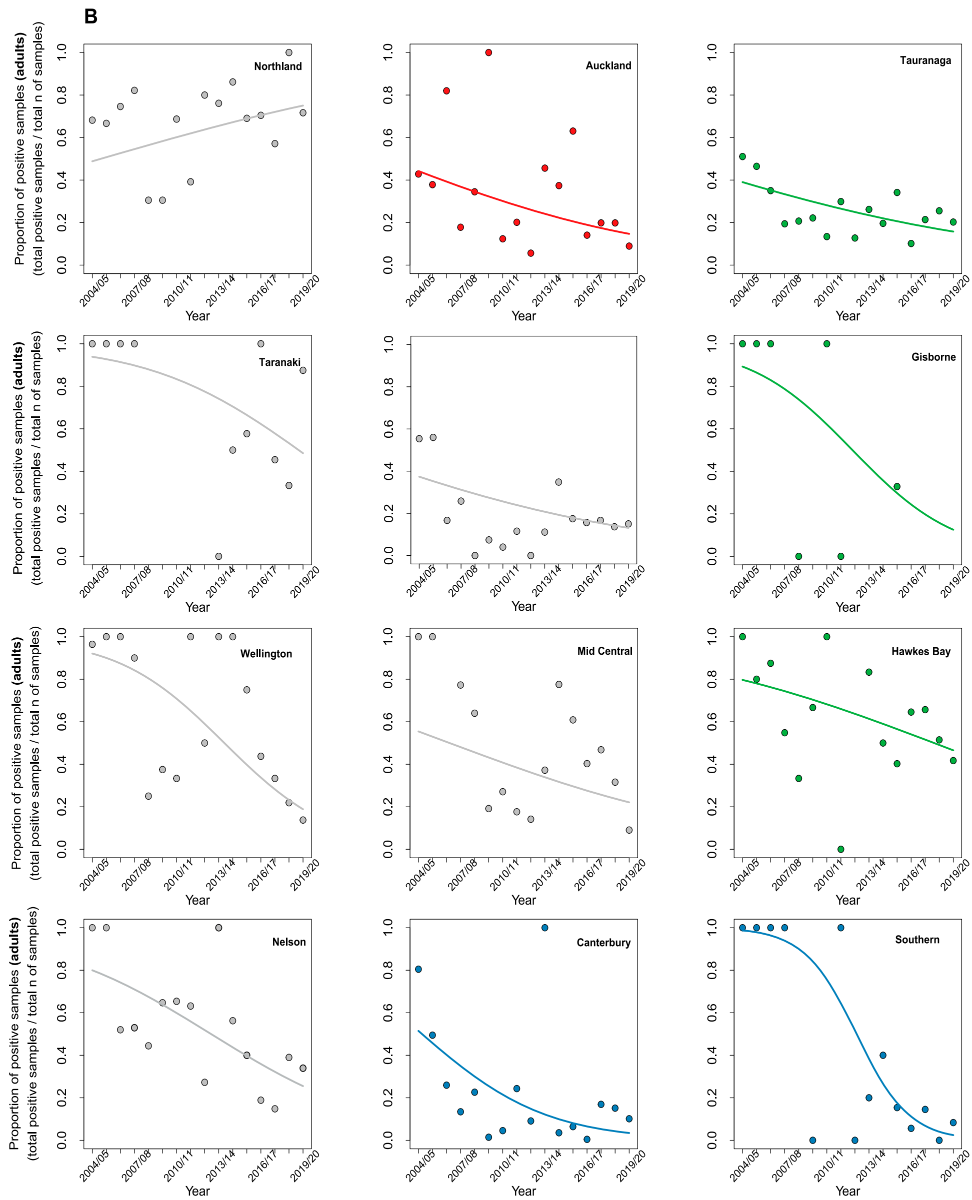

Figure 2. Continued.

Auckland and East clusters in 2004; but by 2019–20 sampling success rates for adults had markedly increased to over 80% for adults in both North Island clusters. (Figure 4C and D).

Specimen numbers per sample of Culex pervigilans *and* Cx. quinquefasciatus

In larva samples, a significant three-way interaction between year, location and species accounted for the number of individual *Cx. pervigilans* and *Cx. quinquefasciatus*

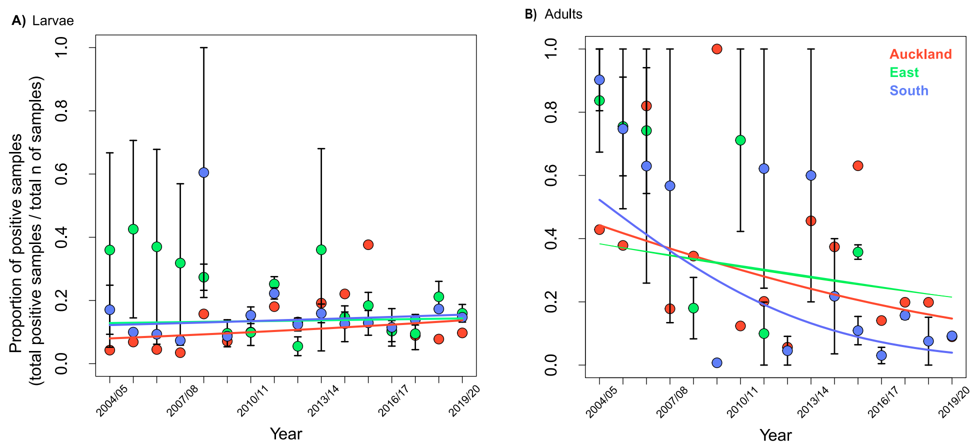

Figure 3. Proportion of samples positive for mosquitoes according to sampling effort by clustered area (Auckland, East and South) between 2012 and 2020. **A,** Larvae; **B,** adults.

specimens in the samples (scaled deviance = 28.09, df = 2, n = 192, $p < 0.05$). Thus, the change over time and the number of specimens varied depending on the location and this relationship between time and location. This also varied between the two species (Figure 5). *Cx. pervigilans* (both larvae and adults) were generally low in number in each sample, approx. 1–5. (Figure 5A and C).

With adult samples, there was a significant interaction between location and species (scaled deviance = 6.80, df = 2, n = 192, $p = 0.03$) and an additive significant effect of year (scaled deviance = 11.66, df = 1, n = 192, $p < 0.05$). Within a general decrease of adult numbers over time, the specific patterns and proportions of each species varied by location. In explicit terms, this meant that despite a drastic increase in the sample success for *Cx. quinquefasciatus* larvae in Auckland, the actual numbers in each sample remained consistently low. There was a linear increase of sample success accompanied an exponential increase in the number of samples from the East grouping around the 2016/17 season, with a similar exponential spike observed later in the South, around 2019/20. (Figure 5A). This exponential incline in adult sample success reflects the sudden occurrence of *Cx. quinquefasciatus* in the south where it had previously been absent. (Figure 5D).

Discussion

While the primary focus of surveillance at POEs is the detection of exotic container breeders, the National Surveillance Programme in New Zealand covers a plethora of trapping and sampling methods (NZ BioSecure 2019) and monitors different habitats sometimes far beyond the actual POE. Monitoring the abundance of native mosquitoes is a part of the program as it is important to assess potential breeding habitats and the broad efficiency of all monitoring tools. Indeed, both species examined here are indicated as adaptable and opportunistic container breeders (Baber 1934). However, the dataset from the National Surveillance Programme does not cover rural or indigenous environments. Therefore, possible differences regarding biased trapping and sampling success between *Culex quinquefasciatus* and *Cx. pervigilans* are discussed below.

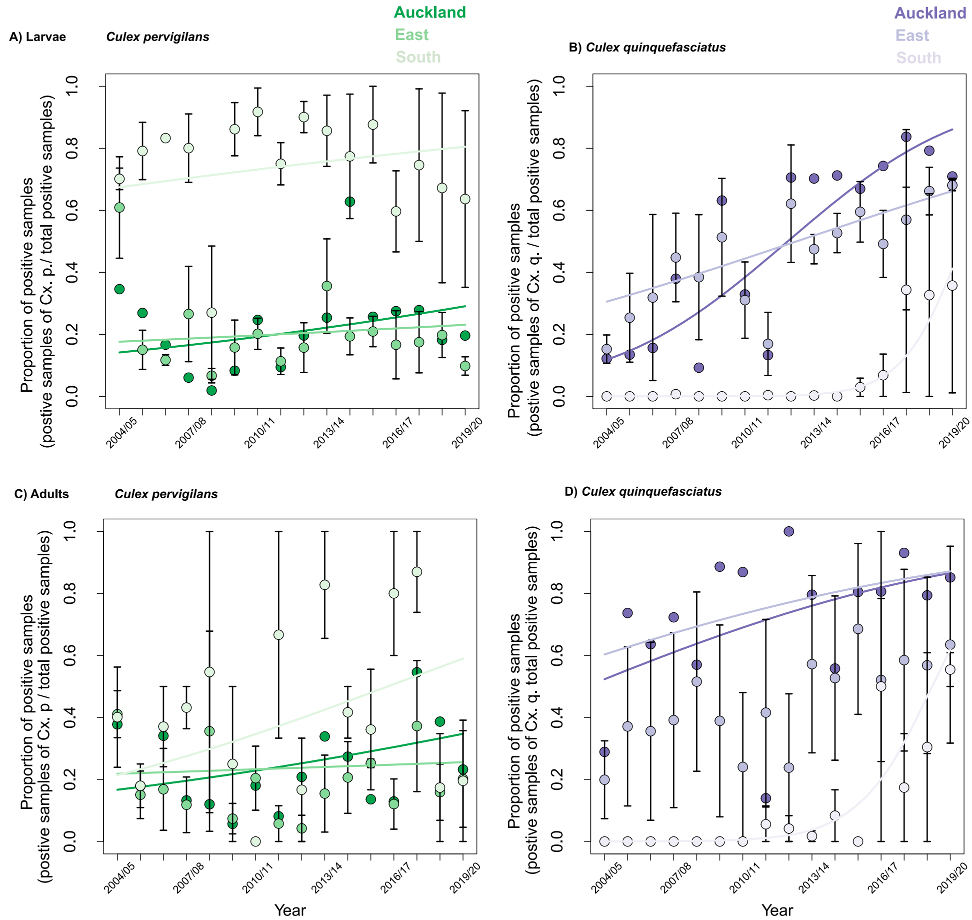

Figure 4. Proportion of positive samples (mean ± range/95% CI) of a native and an invasive sample species in the Auckland, East and South areas between 2012 and 2020. **A,** *Culex pervigilans* larvae; **B,** *Cx. quinquefasciatus* larvae; **C,** *Culex pervigilans* adults; **D,** *Cx. quinquefasciatus* adults.

All tests demonstrated a significant interaction between time and location, or even a three-way interaction between time, location and species. In the former case, variations in catch rate across years depended on locality, while in the latter case, the catch rates varied additionally between the two species. Possible reasons for this and detailed results of the three tested hypotheses are discussed below.

Have mosquitoes in New Zealand increased in general over the last 15 years?

By placing the sample success of *Culex quinquefasciatus* and *Cx. pervigilans* within the context of the catch rate of mosquitoes in general, we can ensure that an increase or decrease in *Cx. pervigilans* or *Cx. quinquefasciatus* numbers is not simply an artefact of an overall change in general mosquito abundance.

Catch rates inevitably reflect the specific trapping and sampling strategies employed by the monitoring project in a particular area, at a given time (e.g. type of traps and their positioning, sampling versus trapping, treatments). As a result, general success

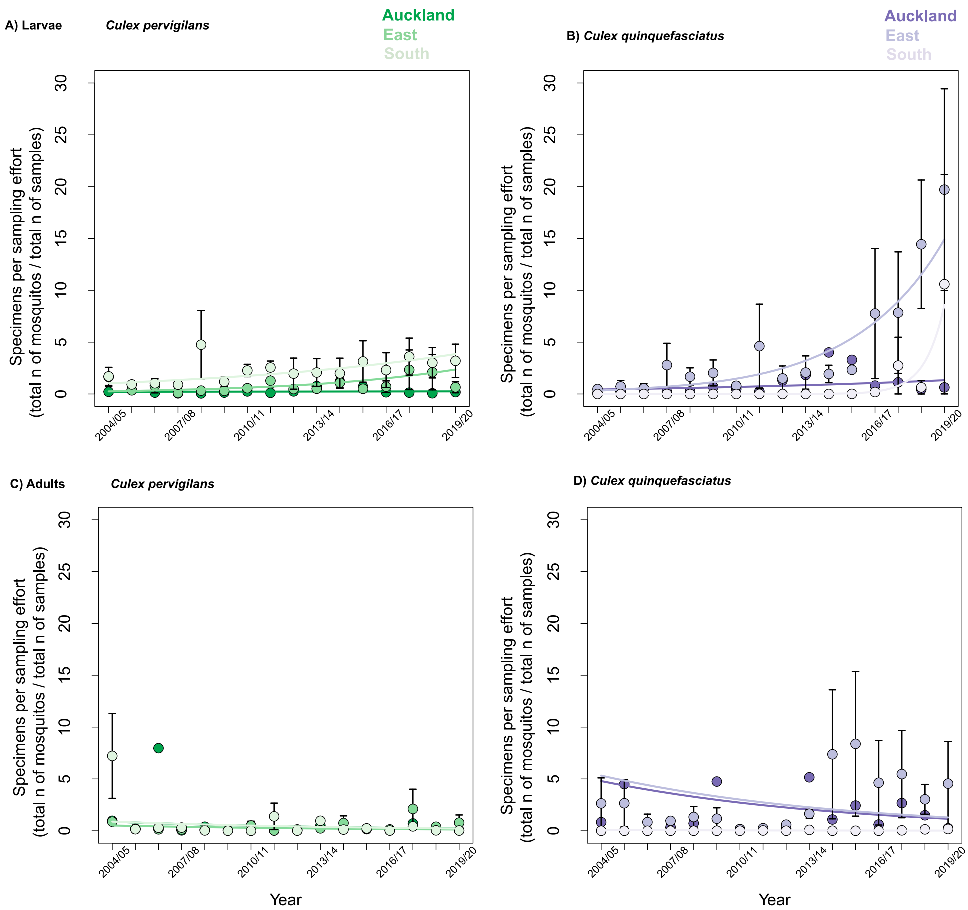

Figure 5. Total mosquito numbers of a native and an invasive species per sampling effort in the Auckland, East and South areas between 2012 and 2020. **A,** *Culex pervigilans* larvae; **B,** *Cx. quinquefasciatus* larvae; **C,** *Culex pervigilans* adults; **D,** *Cx. quinquefasciatus* adults.

rates can, and indeed do, differ considerably year to year. Only in the last 5 years – with more training and experience – has the refined sampling processes (NZ BioSecure 2019) become more consistent across DHBs. This has allowed catch rates to somewhat stabilise, with a downward trend observed (more broadly for adult mosquito samples) (Figures 2 and 3). The decrease of mosquito numbers suggests either a successful long term management of breeding sites in these monitored areas (POEs) or other ecological/economic reasons, further discussed below

Are positive sample rates for Culex quinquefasciatus *increasing independently?*

Despite management efforts and a decline in the general sample success, a significant increase for *Cx. quinquefasciatus* was observed in all locality groupings over time.

This was especially obvious in the East with a conspicuous drop in general sample success, but a linear increase in *Cx. quinquefasciatus* (Figure 4B).

The most striking increase in catch rate, however, was observed with *Cx. quinquefasciatus* larvae in Auckland (Figure 4B).

This could mean the trapping methods have changed, targeting especially *Cx. quinquefasciatus*, but can also suggest a growing population around the POE, and breeding habitats available for intercepted *Cx. quinquefasciatus* allowing allelic invigoration.

Again, this upward trend seen across all other localities likely reflects variable responses to a suite of environmental and ecological factors (that vary in influence by locality).

Is Culex quinquefasciatus *spreading geographically across the country?*

As *Cx. quinquefasciatus* is assumed to have first established in New Zealand in regions within the East grouping (Belkin 1968) it is unsurprising that a high abundance was observed there from the very start. While the general sample success showed a conspicuous drop, *Cx. quinquefasciatus* sample rates increased linearly (Figure 4B) over the sample period. Higher nutrition in the waterbodies, as a result of warmer temperatures and changing land uses, is known to be beneficial for *Cx. quinquefasciatus* due in part to its affinity for and tolerance of these 'dirty' eutrophic habitats. This has likely favoured the species over *Cx. pervigilans* within the context of these ecological changes (Koval and Vazquez-Prokopec 2018).

Cx. quinquefasciatus, as mentioned before, was not thought to be established in lower regions of the South Island; as such, the probability of catching *Cx. quinquefasciatus* in the South grouping was low until the 2015/16 season. A sudden jump in 2017/18 (Figure 4B) confirms our initial theory that *Cx. quinquefasciatus* is indeed spreading southward.

Is Culex quinquefasciatus *in New Zealand increasing in quantity?*

Despite the high number of positive samples of *Cx. quinquefasciatus* larvae in Auckland, the numbers within the samples was consistently low (Figure 5B). The reason for this is likely a product of the region's regular treatment of sumps with Bti (*Bacillus thuringiensis israelensis*). Although more sumps and other waterbodies are sampled in Auckland than in all the other POEs, they are less likely to hold many larvae and a dipper would only catch a few specimens, compared to entire egg batches that develop in a tyre trap, which are mainly indoors at the Auckland airport.

The significant effect that high-order environmental variability (kurtosis) has on mosquito abundance fluctuation is well established (Poh et al. 2019) and this usually stems from two broad climatic pre-determinants: temperature and rainfall (Ahumada et al. 2004; Okiwelu and Noutcha 2011; Lebl et al. 2013).

As such, a spike in the abundance of *Cx. quinquefasciatus* adults during the 2016/2017 seasons in the East grouping (Figure 5B) may be in part attributable to a series of severe flooding events in the region; and subsequent above-average annual rainfall and temperatures across these and following years (NIWA 2018). This may have contributed to the high degree of scaled deviation seen in the region. Interpreted within the context of a clear upward trend in adult population, these results are evidence of a probable, broad, population increase of *Cx. quinquefasciatus* in the East grouping.

In contrast, below-normal annual rainfall across much of the upper and lower South Island in 2016 and 2017 respectively, combined with desiccating, above-average temperatures, may have presented the southern *Cx. quinquefasciatus* populations with particularly unfavourable conditions for their proliferation over this period. The South grouping was itself subjected to a number of severe flooding events and particularly in 2019/2020 above-average temperatures and rainfall across much of the South Island, against low-rainfall, high temperatures in the North Island, may account for the observed spike in abundance across the southern region across that season.

While *Cx. quinquefasciatus* is likely to have already established in parts of the South grouping outside of Christchurch before this point, the exponential increase in adult sampling frequency between 2017 and 2020 is compelling retrospective evidence of a range and/or population expansion in the South grouping and a reflection of current population trends.

Is there any trend evident for **Culex pervigilans?**

The described population trends of *Cx. quinquefasciatus* are only partially mirrored by *Cx. pervigilans* in the monitored urban environments. While the sampling rates for *Cx. pervigilans* only slightly increased over time, they remained lower overall than those observed in *Cx. quinquefasciatus* in the Auckland and East regions (Figure 4A and C). This supports our understanding that *Cx. quinquefasciatus* is innately more suited to urban environments despite *Cx. pervigilans* notably adapting to anthropogenic pressures over the last century. The differences in diet, behaviour and susceptibility to predation and environmental stressors, however, remain. *Cx. pervigilans* can readily utilise a range of breeding habitats, although freshwater pools are their presumed breeding environment (Derraik et al. 2005). Also, tree canopies are suggested to be the preferred mating environment of *Cx. pervigilans* (Derraik et al. 2003), and these are scarce in highly urbanized habitats. These anthropogenic influences favour not only *Cx quinquefasciatus* but also *Aedes notoscriptus*, another introduced metropolitan mammal-biter, and therefore, an additional competitor in urban environments.

Indeed, within this sampling context *Cx. pervigilans* does not appear to respond as dramatically and/or to the same environmental factors as *Cx. quinquefasciatus*, but with seven of the last nine years being some of the warmest on record for New Zealand (NIWA 2022) the broad upward trend in adult sampling success for *Cx. pervigilans* may be in response to this warming (Leisnham et al. 2006).

In the South, the sampling rates for *Cx. pervigilans* larvae is overall higher than seen elsewhere and strikingly we observed a dramatic increase in adult sampling success. It remains to be tested if *Cx. pervigilans* is more or less abundant in rural and indigenous habitats, but as the majority of the New Zealand urban population resides in the North Island, it may be that the increased abundance of *Cx. pervigilans* observed in the southern region data simply reflects an overall lower degree of urbanisation in the southern region and a greater integration of the POEs and other sampled environments with urban centres.

Furthermore, as *Aedes notoscriptus*, and up until recently *Cx. quinquefasciatus*, have been absent in the Southern Region, local *Cx. pervigilans* populations have largely been spared the competition and pressures from introduced container breeders, with the only other well-established exotic species *Ae. australis* (Erichson, 1842) occupying entirely different habitats to *Cx. pervigilans*, namely coastal areas.

Conclusion

What are the potential risks of an invasive species like Culex quinquefasciatus *in New Zealand?*

This study adds to the ever-accumulating evidence that anthropogenic forces are altering the distribution and ranges of mosquitoes in New Zealand.

These findings, indicated by the biosecurity surveillance data, confirm our hypothesis that the prevalence of *Cx. quinquefasciatus* at lower altitudes throughout the North Island is increasing. It additionally suggests a more recent expansion into the South Island. This is observed in the number of positive samples for the species and the counts of larvae obtained per sample increasing across the southern region.

Climatic factors have most likely contributed to the apparent spread of *Cx. quinquefasciatus* alongside an aggravating loss of indigenous forested habitats, and an expansion of urban and peri-domestic habitats favouring this introduced species (Derraik and Slaney 2007).

Whether urbanisation in New Zealand is, in providing favourable conditions for *Cx. quinquefasciatus*, limiting habitat availability for *Cx. pervigilans* is not established. Although it is believed that an invasive adaptable species would replace vulnerable and highly specialised species (McKinney and Lockwood 1999), tending toward a global biotic homogenisation, *Cx. pervigilans* is not suitable to test this hypothesis. The prevalence of *Cx. pervigilans* in the urban environments examined by this dataset suggests that this species is readily breeding in these urban spaces, given limited inter-species competition.

To further appreciate current and potential risks to conservation in New Zealand more extensive surveys are needed to document the occurrence of *Cx quinquefasciatus* in habitats not covered by biosecurity surveillance; notably in residential and recreational areas, on farmland to medium altitudes and especially along current southern and altitudinal distribution limits. The New Zealand mosquito census (Moor et al. 2019; Te Papa 2019) aims to fill these gaps, and if conducted over a sufficient period would provide geo-temporal confirmation of these trends.

However, understanding the urban mosquito populations provides a vital point of reference when assessing changes and in anticipating the spread of human or avian pathogens (Tompkins et al. 2013). *Cx. quinquefasciatus* is a vector for a range of human diseases, namely: dengue, filariasis, Ross River, Japanese encephalitis, chikungunya and West Nile with variable competency, but all of concern in New Zealand (Ministry of Health, 2021). The recent outbreak of Japanese encephalitis in Australia is a timely reminder of why this is (Australian Government Department of Health 2022). The continued expansion of global trade, warming, and travel are all identified as aggravating factors in the risk of incursion and establishment by exotic mosquitoes and pathogens (Samy et al. 2016).

Unwanted exotic mosquitoes arriving with aircraft and freight have been the principal focus of border control and surveillance efforts in New Zealand to date; representing both a probable and manageable route of entry for vector-borne disease (Biosecurity Act 1993; NZ BioSecure 2019). But, the increasing number of viraemic persons regularly entering New Zealand highlights the permeability of its border to human movements, and represents another increasingly likely modus of entry (Ammar et al. 2021). This increases

Table 2. Interception response for *Culex quinquefasciatus* (July–June).

Annual period	Responses	Specimens (n)
2005–06	5	32
2006–07	7	171
2007–08	3	8
2008–09	17	54
2009–10	16	72
2010–11	18	127
2011–12	4	65
2012–13	11	38
2013–14	11	35
2014–15	20	82
2005–16	42	65
2016–17	38	57
2017–18	23	33
2018–19	19	22
2019–20	9	14
2020–21	16	53

both the frequency and likelihood of exposure of established mosquito species, such as *Cx. quinquefasciatus*, to pathogens.

Extended mosquito–human–mosquito cycles of direct transmission in densely populated areas are often observed with outbreaks of dengue fever (Thongsripong et al. 2021) and other arboviruses (Filho et al. 2019); which considered together with the above factors, challenges the long-held presumption that our resident mosquito populations will remain unimplicated. As such, the range and quantity expansion exhibited by in this study warrants some concern and investigation.

In addition to human health concerns regarding the transmission of arboviral disease in New Zealand, *Cx. quinquefasciatus* presents concerns for conservation as a competent vector of both avian malaria (*Plasmodium*) and avian pox virus (Harvey-Samuel et al. 2021). The former was described as early as 1950 in New Zealand (Laird 1950), and both were likely imported by migratory and introduced birds (Alley MR et al. 2010). Avian malaria primarily infects passerine birds and is a substantial threat to the immunologically naïve native birds which have evolved in geographic isolation as in New Zealand. There are confirmed cases linked with the deaths of endemic species including Yellowhead (*Mohua ochrocephala* (Gmelin, 1789)), Kēreru (*Hemiphaga novaeseelandiae* (Gmelin, 1789)), Kiwi (*Apteryx*), Saddleback (*Philesturnus*), and a number of non-native passeriforms which may be acting as reservoir species for the pathogens involved (Schoener et al. 2014).

In Hawaii, similar to New Zealand in its isolation, avian malaria (*Plasmodium relictum*) has been implicated in the widespread decline and the possible extinction of many species (Warner 1968; van Riper et al. 1986). Transmission of this parasite was not possible until a competent vector, i.e. *Cx. quinquefasciatus*, was introduced in 1826 (Warner 1968). The pathogen is maintained in competent and abundant mosquito populations, and a disease reservoir of chronically infected native birds. Global warming is expected to increase the elevational limit that provides some refuge from infection and is the key to survival of some susceptible birds. Increased temperatures may have already increased global avian malaria prevalence and contributed to the emergence of avian disease in New Zealand. There is also anecdotal evidence of Avian Pox virus transmission by *Cx. pervigilans,* which would greatly increase the potential or current distribution of this pathogen in New Zealand.

Since *Cx. quinquefasciatus* is highly variable globally, with multiple strains differing in habitat and host preferences as well as vector competency, it is important to establish whether there have been, or indeed are, repeated introductions of these strains to New Zealand. Although Cane et al. (2020) found no clear evidence of population variation in New Zealand on the basis of molecular barcodes; the MOH National Mosquito Surveillance Programme has recorded multiple suspected interceptions of unclear origin or source population at the sea and airports in Wellington, Christchurch, Tauranga and especially in Auckland (Ammar et al. 2019; NZB-Border Health Newsletter; Farr 2000) (Table 2). As such, closer investigation and ongoing genetic surveillance of these *Cx. quinquefasciatus* populations around POEs is warranted. This type of monitoring will provide vital context for the risk assessment of what would be an otherwise overlooked health concern.

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