Invasion potential of the island sugarcane planthopper, Eumetopina flavipes (Hemiptera: Delphacidae): vector of Ramu stunt disease of sugarcane

Thesis submitted by

Kylie Lucille Anderson B.Sc. (Hons) JCU Qld

In

2011

For the degree of Doctor of Philosophy

in the School of Marine and Tropical Biology

James Cook University

ACKNOWLEDGEMENTS

Sincere thanks to:

My amazing husband Rob for his support through thick and thin, our son Christian and my mum Denise.

My supervisory committee. Brad Congdon at JCU who inspired me to begin, and whose extraordinary supervisory skills and ongoing support enabled me to complete. Nader Sallam at BSES Ltd, whose technical expertise and contacts were invaluable and utterly essential for successful completion. Myron Zalucki at UQ, whose time and advice have been ever-present and much appreciated.

My JCU cohort, Anna Koetz, Sandra Abell-Davis, Petrina Johnston, Tamara Ball, Karen Benn, Carol Erwin, Romina Rader and Luke Rapley. Thanks for listening and for all your advice. Couldnadunitwivoutya!

BSES Ltd staff, particularly Ann Rizzo who was ever-present and enthusiastic, Rob Magarey (whose input was invaluable for successfully completing the complementary ACIAR project) and David Donald.

The Torres Strait Regional Authority, Island Coordinating Council, Torres Strait Island Regional Council and Northern Peninsula Area Regional Council (particularly Mayor Jesse Sagaukaz), and all Torres Strait and northern peninsula area traditional owners for assistance and permission to conduct field work. Especially to all keen gardeners throughout the Torres Strait, particularly Albert Bond at New Mapoon. I am still really sorry I interrupted your lunch that day. Survey participants and volunteers in the TS/NPA: Jamie Seymour, Sam Price-Rees, Rob Anderson, and PNG: Kaile Korowi, Lastus Kuniata and Sarah Naemon (Ramu Agri-Industries Ltd).

Tom and Gaynor Watters for carefully tending a patch of badila cane for four years at their Meringa cane farm. Also to Tom for agreeing to appear in my *Bugger Off with Metapopulation Theory* video.

The JCU support team, particularly Leanne Shillitoe, Eva King, Sue Kelly, Anita Christian and Lynn Jones.

Australian Quarantine Inspection Service staff James Walker, Barbara Waterhouse, Kerrie Huxham, Tim Kerlin and Louise Hucks. Also to the marvellous trio of Jackson Sailor, Jimmy Bond and Eric Cottis at Bamaga, Cygnet Repu (Mabuiag), Clayford Lui (Yam), and Stan and Gadu Banu (Boigu), James Bon (Mer), Hildy Mosby (Yorke), Jack Billy (Coconut), Roy Ahwang (Horn). Marybeth Gundrum, Andrew Gordon, Judy Grimshaw and Anthony Rice.

Jacqueline Balston (Jacqueline Balston and Associates), Averil Hogan (Freelance Graphic Design), Michael Porta, Mick Callen and Peter Allsopp (BSES Limited), Scott Ritchie and Kylie Brown (JCU), John Stephen (AGRF Adelaide), Aaron Jackson (NPA College), Stephen Amber (Hammond Community Council Ranger), and Greg Malone (Muralug).

Funding was provided by 1) Sugar Research and Development Corporation (PhD Scholarship, operating funds and supporting participation at skills development workshops), particularly Tracey Henderson and Diana Saunders; 2) The Australian Centre for International Agricultural Research.

This research complied with all Ethics requirements and Australian laws and standards.

PUBLICATIONS ARISING

Chapter two:

Anderson, K.L., Sallam, M. & Congdon, B.C. 2007. Long distance dispersal by *Eumetopina flavipes* (Hemiptera: Delphacidae), vector of Ramu Stunt: Is Culture Contributing? *Proceedings of the Australian Society of Sugarcane Technologists* 29: 226-234.

Chapter three:

Anderson, K. L., Deveson, E. D., Sallam, N. and Congdon, B. C. 2010. Wind-assisted migration potential of the island sugarcane planthopper, *Eumetopina flavipes* (Hemiptera: Delphacidae): implications for managing incursions across an Australian quarantine frontline. *Journal of Applied Ecolo*gy 47: 1310-1319 (IF = 4.97).

Chapter four:

Anderson, K. L., Sallam, N. and Congdon, B. C. 2009. The effect of host plant structure on the distribution and abundance of the island sugarcane planthopper, *Eumetopina flavipes* Muir, vector of Ramu stunt disease of sugarcane. *Virus Research* 141(2): 247-257 (IF = 2.905).

Chapter five:

Anderson, K. L. and Congdon, B. C. In review. Reconciling invasion route and dispersal mechanisms with population genetic characteristics of a quarantine pest. *Molecular Ecology* (IF = 6.457).

.

SUMMARY OF GRANTS AND AWARDS

2010.....Winner. Best oral presentation in the Applied Ecology Session. James Cook University School of Marine and Tropical Biology Conference. AUD500.

2010.....James Cook University Graduate Research School Travel Award. AUD1220.

2009.....Winner. The Phil Carne Prize. Best entomological research by an early career scientist, awarded by the Australian Entomological Society. AUD1300.

2005 – 2010....Sugar Research Development Corporation PhD Scholarship AUD78,000.

2005 – 2010....Sugar Research and Development Corporation Operational Funds AUD52,178.

2006 – 2008....Australian Centre for International Agriculture Research AUD84,740.

2008.....Sugar Research Development Corporation Travel and Learning Opportunity Project AUD4058.

2007.....Australian Quarantine and Inspection Service Research Grant AUD1200.

2007.....James Cook University School of Marine and Tropical Biology Travel Award. AUD2000.

2007.....Winner. James Cook University Inaugural Graduate Research School Postgraduate Poster Competition. Return airfare to Singapore and five nights accommodation.

2007.....Honorarium. Invited paper presented at the 10th International Plant Virus Epidemiology Symposium, Hyderabad, Andhra Pradesh, India. IRP2500.

2007.....Winner. H. William Kerr Memorial Award and Bursary. Best student paper presented in the agriculture session of the 29th Australian Society of Sugarcane Technologists Conference, Cairns. AUD400.

2006.....Sugar Research Development Corporation Travel and Learning Opportunity Project AUD5000.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

THESIS ABSTRACT

The island sugarcane planthopper, *Eumetopina flavipes* Muir (Hemiptera: Delphacidae) is the only known vector for Ramu stunt disease of sugarcane. Ramu stunt disease appears confined to PNG, but disease-free populations of *E. flavipes* are known to occur throughout the Torres Strait island archipelago and on the northern peninsula area of Cape York, Queensland, Australia. The presence of these populations represents a significant threat to the commercial production of sugarcane in Australia, which occurs approximately 700 km south of the *E. flavipes* populations on the northern peninsula area of Cape York, Queensland.

In order to mitigate the risk of *E. flavipes* and/or Ramu stunt disease invasion into Australia through the Torres Strait, and to contribute to the development of a management program for *E. flavipes* populations in the Torres Strait, there is a need for a detailed understanding of the mechanisms which drive *E. flavipes* invasion success in the Torres Strait.

Anthropogenic movement of infested sugarcane was hypothesised to be important for initial dispersal into, as well as recolonisation of populations throughout the Torres Strait. The ability of mobile life stages of *E. flavipes* to survive over time on cut sugarcane stalks was assessed. Whilst nymphs and adults leave the stalk at different rates over time, almost half of the initial population of nymphs and almost one third of the adults survived six days *in-situ* on cut stalks. *E. flavipes* is therefore capable of surviving extended periods of time on deteriorating host plant material, implying that human mediated movement of cut stalks may play an important role in the dispersal of *E. flavipes*.

In addition to the anthropogenic movement of infested sugarcane, long-distance, wind-assisted immigration from Papua New Guinea may be responsible for the continued presence of *E. flavipes* in the Torres Strait and on the tip of north Queensland. Simulation was used to predict *E. flavipes* wind-assisted immigration potential from Papua New Guinea into the Torres Strait islands and mainland Australia. Field studies were used to test the predictions. Wind-assisted immigration from Papua New Guinea was predicted to occur widely throughout the Torres Strait islands and the tip of mainland Australia, especially in the presence of tropical depressions and cyclones.

Simulation showed potential for a definite, seasonal immigration which reflected variation in the onset, length and cessation of the summer monsoon. In general, simulation predictions did not explain *E. flavipes* observed infestations. The discrepancy suggests that post-colonisation processes such as the temporal and spatial availability of host may be equally or more important than possible wind-assisted immigration in determining population establishment, persistence and viability.

For phytophagous insects like *E. flavipes*, the distribution and abundance of host plants is highly important in regulating establishment, growth and population persistence. The relationship between host plant distribution and abundance, and *E. flavipes* distribution, abundance and levels of population connectivity in the native range Papua New Guinea, and the introduced region of the Torres Strait and northern peninsula area of Cape York, was established. *E. flavipes* uses a wide range of *Saccharum* host species in Papua New Guinea, and occupancy rates and abundances differ significantly among host types. For hosts in common to both Papua New Guinea and Torres Strait, the proportion of plants occupied in Papua New Guinea was significantly greater than in Torres Strait. This is likely to be the result of greater overall host plant density and connectivity in Papua New Guinea. *E. flavipes* abundance per plant did not differ significantly between the two regions suggesting a possible plant-specific abundance and/or dispersal threshold independent of location. Whilst *E. flavipes* presence and persistence was highly variable at some Torres Strait locations, large and stable infestations occurred along the western edge of the Torres Strait archipelago. These populations appear to link Papua New Guinea to the northern peninsula area, and offer a potential incursion route for Ramu stunt disease. The stability of these populations appears to be associated with the availability and persistence of host plants, which in turn is significantly affected by location-specific variations in cultivation practices.

Information on hypothesised dispersal mechanisms was combined with analyses of population genetic structure to investigate the invasion dynamics of *E. flavipes* through the Torres Strait. Analysis of data from eight microsatellites in 648 individuals suggest that frequent, wind-assisted immigration from multiple sources in Papua New Guinea contributes significantly to repeated colonisation of Torres Strait islands close to Papua New Guinea. In contrast, intermittent long-distance, wind assisted immigration better explains patterns of genetic diversity and structure in the southern Torres Strait and on the tip of mainland Australia. Significant genetic structuring associated with the

presence of clusters of highly related individuals occurs throughout the region. In general, this suggests that following colonisation by small numbers of individuals, population growth on each island is kin-structured with little post-establishment movement. There is some evidence that secondary movements between islands are restricted by quarantine zones. Control of the planthopper may be very difficult on islands close to Papua New Guinea given the propensity

Results suggest that implementation of pre-emptive management of *E. flavipes* via particular cultivation techniques, such as the simultaneous tip-pruning of all sugarcane plants in the area, may be an effective means of control and/or eradication for the pest in parts of the Torres Strait. Eradication of *E. flavipes* from northern Torres Strait islands appears unlikely given the propensity for annual invasion, but may be achievable further south where local populations appear highly independent and isolated.

The creation of a planthopper-free buffer zone in the southern Torres Strait would serve to reduce the invasion threat to commercial Australian sugarcane. Pre-emptive management of *E. flavipes* in the Torres Strait islands and on the northern peninsula area of Cape York, Australia, is thus recommended using the strategy outlined in this thesis. Pre-emptive management of *E. flavipes* would be simpler and preferable to the direct management of Ramu stunt disease should it be detected in the Torres Strait.

CHAPTER 1 GENERAL INTRODUCTION

1.1 THESIS RATIONALE

The environmental and economic costs of biological invasions are key issues for many countries (Pimentel *et al.* 1999). Australia's international position as a primary industry and export-based economy means that it is vital to maintain 'area freedom' from the devastating pests and diseases present in many other countries. There have been a number of new pest incursions into Australia from the northern neighbouring countries of Papua New Guinea (PNG), Indonesia and Timor Leste in the past ten years, with these generally coming at a high cost. For example, the ensuing eradication effort following the detection of papaya fruit fly in Cairns, Australia, in 1995 cost an estimated $33 million over 4 years (Cantrell *et al.* 2002).

Preparedness may assist in avoiding expensive *post-hoc* and reactionary responses to new invasions (Leung *et al.* 2002). Much difficulty lies in attempting to identify which of the myriad exotic pests and diseases could potentially become a major problem should an incursion occur, the most likely incursion pathway for a particular pest, and the specific background ecological conditions that may either facilitate or impede an incursion.

There are three recognised critical stages that occur during the invasion process, being transport, establishment and spread (Lockwood *et al.* 2007). Invasive species are transported to new regions in a number of ways. Active participation in long-distance migrations with the assistance of prevailing seasonal winds can result in movement over vast distances (Dingle 1996). Alternatively, invasion may simply be the result of progressive range expansion via diffusion (Lubina & Levin 1988). In recent times, an increasing number of invasions have been the direct result of human-assisted introductions well beyond the invasive species endemic range (Williamson 1996). The use of different transport mechanisms may contribute differently to invasion success because they promote relatively different levels of propagule pressure; that is, how many individuals are transported and how often. High propagule pressure is thought to

be a major determinant of early invasion success as it enhances the likelihood of establishment and persistence (Simberloff 2009).

Habitat availability is important in determining invasion success during establishment and spread (Simberloff 2009). This is especially true for organisms with specific habitat requirements and low mobility (Hanski & Gilpin 1997). If host plants are patchy and widely dispersed relative to the species mobility, they become more difficult to locate, compromising colonisation (Thomas & Hanski 1997). On the other hand, if colonisation is successful, large distances between host plants can result in low levels of dispersal, or connectivity, between populations (Thomas & Hanski 1997), which in turn may contribute to population decline and even extinction (Thomas 2000). In addition, if host plants are very patchy at an invasion front, spread may be very slow, or unlikely (Lockwood *et al.* 2007).

Information on factors contributing to invasion success may be obtained through detailed studies into the ecology of an invading pest; information that may contribute to the formation of management plans to assist in either limiting new invasions or reducing spread in the case of existing incursions.

Ramu stunt is a devastating, systemic disease of sugarcane that occurs in PNG and is caused by an as yet unidentified virus (Waller *et al.* 1987; Magarey *et al.* 2002; Braithwaite *et al.* 2007). In 1986, Ramu stunt disease almost destroyed the fledgling commercial sugarcane industry in PNG, when two of the three main commercial sugarcane cultivars proved highly susceptible to the disease (Waller *et al.* 1987; Eastwood 1990). Currently, Ramu stunt is one of the major diseases affecting commercial sugarcane production in PNG (Kuniata *et al.* 2006). Fortunately, the disease does not occur in Australia, but virus-free populations of the only known insect vector, the island sugarcane planthopper, *Eumetopina flavipes* Muir (Hemiptera: Delphacidae), occur in the 'spindle-roll', or apical leaf-rolls, of sugarcane grown for cultural purposes throughout the Torres Strait islands (TS) and in communities on the northern peninsula area (NPA) of Queensland, Australia (Kuniata *et al.* 1994; Magarey *et al.* 2002).

The Torres Strait is one of the most highly regulated quarantine regions in Australia, partly because there are a number of unique transport mechanisms operating in the region that may facilitate exotic species introductions. The risk of pest and disease incursions into Australia is heightened by the level of people moving through the region, the natural dispersal of organisms through the TS/NPA, and the close

proximity of PNG to mainland Australia. Each of these factors is hypothesised to influence the ability of *E. flavipes*, as well as a number of other invasive pests and diseases, to move around the region.

E. flavipes appears to feed specifically on *Saccharum* L., especially *S. officinarum* L. ('noble' sugarcane) and *S.* 'hybrids' (commercial sugarcane) (Kuniata *et al.* 1994). Throughout PNG, *S. officinarum* is a 'native-domesticated' sugarcane that is traditionally cultivated in domestic gardens alongside a variety of other subsistence food plants such as sweet potato, yam, papaya, cassava and banana (Brandes 1956). Subsistence agriculture has long been a way of life for Melanesian communities, and today most families in PNG still maintain a garden that contains subsistence food plants. A similar situation occurs in the TS/NPA, where *S. officinarum* and *S.* 'hybrids' are cultivated in garden patches, but in general, subsistence gardening is less prolific in the TS/NPA than in PNG. Besides TS/NPA locality records collected during quarantine plant health surveys indicating patchy presence of *E. flavipes* in the Torres Strait, very little is known about *E. flavipes* general biology and ecology, despite it being the only known vector for Ramu stunt disease.

The northern-most edge of Australian commercial sugarcane plantations are approximately 700 km south of the *E. flavipes* populations that occur on the NPA. At the time of writing, the gross 2010/2011 value of commercial Australian sugar production was forecast to be around A$1.69 billion (Foster 2010). Approximately 30% of all commercially grown sugarcane varieties in Australia are susceptible to Ramu stunt disease (Dr Robert Magarey, BSES Ltd., *pers. comm.*). Based on these figures, approximately A$500 million export sugar may be at risk should Ramu stunt disease establish in commercial sugarcane plantations.

For an organism to be considered a 'threat', it must pass through each of the recognised invasion phases; these being transport, establishment and spread, and then have the capacity to cause either ecological or economic harm (Lockwood *et al.* 2007). *E. flavipes* has clearly passed through each invasion stage to be present in the TS/NPA, and the relative close proximity of *E. flavipes* populations in the TS/NPA to commercial plantations on mainland Australia poses a high risk quarantine threat to the production of commercial Australian sugar. Therefore, *E. flavipes* status as a pest of significant quarantine concern justifies research that will assist in developing a management plan to prevent new invasions and limit further spread.

In order to mitigate the risk of *E. flavipes* and/or Ramu stunt disease invasion into Australian sugarcane plantations, and contribute to the formation of a comprehensive management plan for *E. flavipes* in the TS/NPA, there is a need to investigate the processes that contribute to *E. flavipes* invasion success through the Torres Strait.

In bringing ecological information into management recommendations, this work has relevance to other invasive or pest species where efforts are being made to limit their spread beyond particular boundaries.

1.2 AIMS AND THESIS STRUCTURE

The overall aim of this thesis is to investigate the relative importance of factors which contribute to *E. flavipes* overall invasion success in the TS/NPA. This was achieved by breaking the overall aim into a number of distinct studies.

1. To determine *E. flavipes* potential for both large and small scale dispersal from PNG into and around the TS/NPA,

2. To determine the effect of host plant availability on the population structure of *E. flavipes* in the TS/NPA,

3. To determine the relative importance of pre- versus post- invasion processes that contribute to *E. flavipes* invasion success in the TS/NPA.

The final aim of this research was to synthesise results, and:

4. To develop an appropriate management plan for *E. flavipes* in the TS/NPA, so that control measures may be implemented at the appropriate stage of invasion.

In this first introductory chapter, the general theoretical and applied background and rationale for the research has been outlined. Each of the following data chapters (chapters two to five) include an introduction to the literature and general background as it relates to the specific research questions being addressed. As each data chapter has

been peer-reviewed and published (excluding chapter five, which is in review), they are effectively self-contained, and the thesis is designed so that each data chapter naturally builds on from the knowledge gained in the previous chapter.

Chapters two and three investigate the likelihood and potential for large-scale dispersal by *E. flavipes* via the two most likely transport mechanisms, anthropogenic movement of infested sugarcane and long-distance, wind-assisted immigration from PNG. Thus, pre-invasion processes which may contribute to invasion success are examined. Chapter two briefly introduces relevant aspects of the problem at hand and the study region, but focuses on anthropogenic movement via infested sugarcane. Could *E. flavipes* hitch-hike on sugarcane being moved by people? And survive? A transportation event is simulated, and results will indicate whether human-mediated movement is a plausible dispersal mechanism for *E. flavipes*. The aim of chapter three is to investigate *E. flavipes* potential for long-distance, wind-assisted immigration from PNG into the TS/NPA. Computer simulation will be used to predict *E. flavipes* potential distribution and abundance in the TS/NPA, whilst field studies are used to test the model predictions.

Once an organism has successfully arrived in a new location, it must establish. For host-specific organisms such as *E. flavipes*, the distribution and abundance of host plants is a potential major determinant of successful colonisation, population growth and ongoing persistence. The purpose of chapter four is to derive a detailed spatial and temporal picture of the influence of differing host plant availability in PNG and TS/NPA, on *E. flavipes* distribution and abundance throughout both regions. This objective is a critical step in establishing the post-invasion success of *E. flavipes* in the TS/NPA.

Chapter five overlays spatial patterns of population genetic diversity and connectivity throughout the TS/NPA on to results from the previous chapters, to build insight into *E. flavipes* invasion history and the relative importance of pre- versus post-invasion processes in determining *E. flavipes* overall invasion success.

The general discussion in chapter six provides a synthesis of all major findings, and outlines the final recommendations for management of *E. flavipes* in the TS/NPA. Finally, limitations encountered during the study and suggestions for further research are discussed.

Note: Citation of any publication arising from this thesis is coupled in parenthesis with a reference to the appropriate chapter.

CHAPTER 2 ANTHROPOGENIC MOVEMENT POTENTIAL

Publication Arising:

Anderson, K.L., Sallam, M. & Congdon, B.C. 2007. Long-distance dispersal by *Eumetopina flavipes* (Hemiptera: Delphacidae), vector of Ramu stunt: is culture contributing? *Proceedings of the Australian Society of Sugarcane Technologists* **29,** 226-234.

2.1 INTRODUCTION

The likelihood that a species will successfully colonise a new region is dependent upon a variety of pre- and post-invasion ecological processes. Primary amongst the pre-invasion processes is the ability to reach new locations. This ability may be enhanced through the use of particular dispersal mechanisms (Williamson 1996; Ruiz & Carlton 2003). Should the dispersal mechanism promote high propagule pressure, then successful arrival, establishment, persistence and spread is far more likely (Grevstad 1999; Simberloff 2009).

Many studies have focused on post-invasion determinants of establishment success, and not on pre-invasion processes (Kolar & Lodge 2001; Puth & Post 2005). If the relative importance of different dispersal mechanisms used by a particular pest is well understood, there may be a chance to disrupt these mechanisms and so reduce the risk of new invasions or recolonisation (Carlton & Ruiz 2005). Such pre-emptive management is always preferable due to the expense involved in *post-hoc* reactive control and eradication (Leung *et al.* 2002; Hulme 2006).

A number of dispersal mechanisms that may facilitate invasive species movement into Australia have been noted (Stanaway *et al.* 2001; Pheloung 2003; Lintermans 2004; Floerl & Inglis 2005). One pathway into northern Australia is from Papua New Guinea (PNG) through the Torres Strait islands (TS) (Fig. 2-1). The Torres Strait encompasses approximately 48, 000 km^2 between the southern coast of PNG and the tip of Cape York, Queensland, Australia. There are over 250 islands in the Torres Strait, 17 of

which are permanently occupied by traditional Torres Strait Islander peoples of Melanesian origin, for whom subsistence agriculture is a way of life (Harris 1977; Bourke 1990).

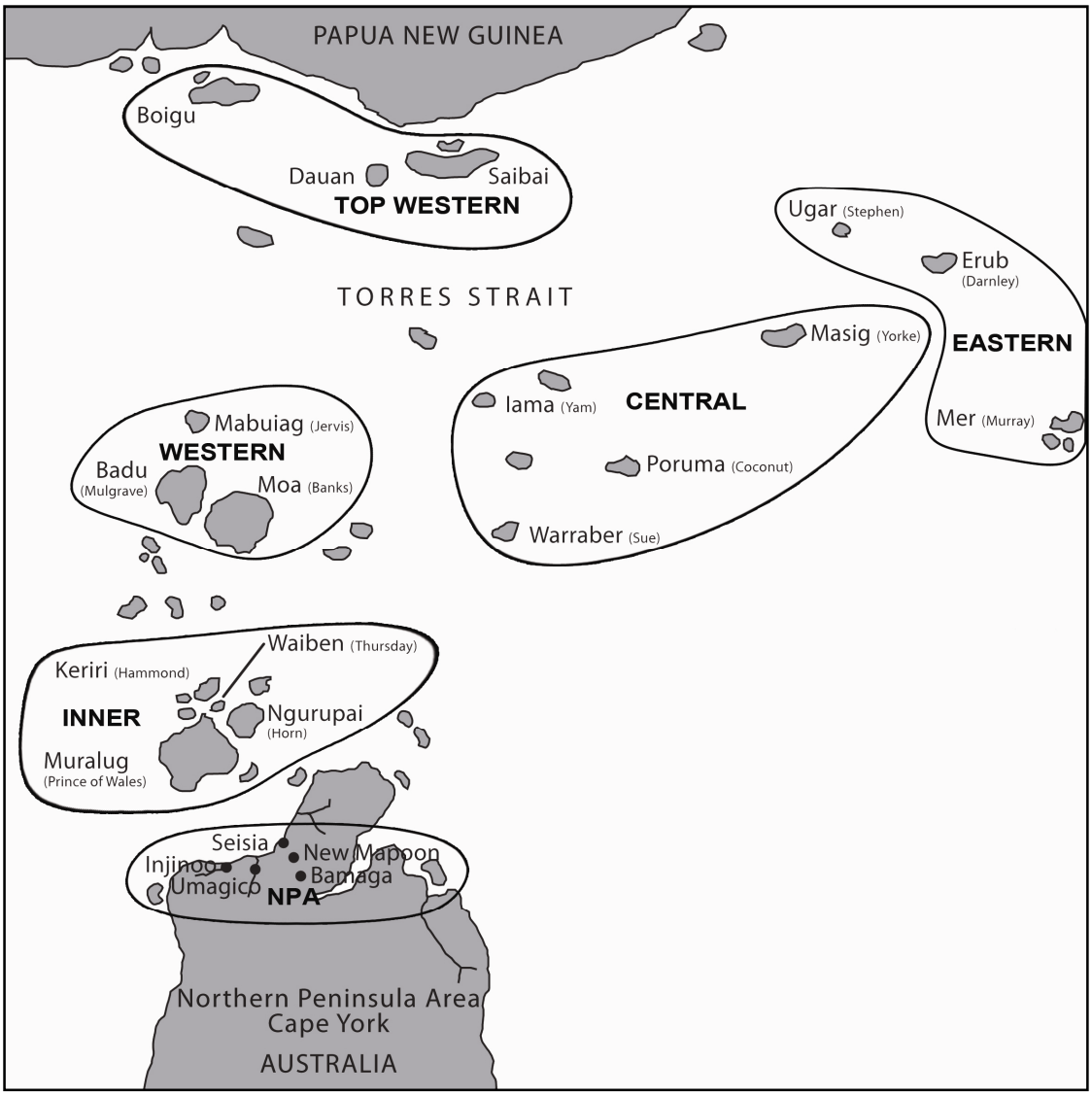


Figure 2-1. Map of southern Papua New Guinea and Torres Strait and northern peninsula area of Queensland, Australia, showing traditional island/community groups. These groups are *Top Western* - Boigu, Saibai, Dauan; *Eastern* - Ugar, Erub, Mer; *Central* - Masig, Iama, Poruma, Warraber; *Western* - Mabuiag, Badu, Moa (Kubin), Moa (St Pauls); *Inner* (Thursday Island) - Waiben, Keriri, Muralug, Ngurupai, *NPA* – Seisia, New Mapoon, Bamaga, Umagico and Injinoo.

The tip of mainland Australia is referred to as the northern peninsula area (NPA) of Cape York, Queensland, where a further five communities of Torres Strait islander as

well as mainland Aborigines occur; these communities being Seisia, New Mapoon, Bamaga, Injinoo and Umagico. Islands/communities are clustered into groups based loosely upon geography and cultural relationships (Fig. 2-1). In keeping with Melanesian traditions, varying degrees of subsistence agriculture occur in both the TS and NPA. Back-yard gardens often contain a mix of plants that may act as hosts for exotic pests and diseases that are not present in commercial production areas on mainland Australia.

The TS are of major concern to Australian quarantine authorities because of the unique variety of potential dispersal mechanisms (Walker 1972; Kikkawa *et al.* 1981; Lindsay 1987). Very little empirical information exists on the specific mode of operation of different mechanisms, their relative importance, and whether successful establishment could result from invasive species using them.

Plants are often deliberately transported by people (Mack & Lonsdale 2001), and many organisms are introduced accidentally into new localities as hitch-hikers on such material (Mack *et al.* 2000). Domesticated sugarcane originated and diversified in PNG (Blackburn 1984), and it is reasonable to assume that when Papuans of Melanesian descent inhabited the northern TS islands several thousand years ago (Barham 2000), they brought subsistence agriculture items like sugarcane. The social custom of exchanging food among Torres Strait Islanders is termed *tama* (Haddon 1908), and has likely been occurring over some 3000 years of human habitation (Lawrence 1994; Carter 2001). Historically, noble sugarcanes were frequently traded and gifted within and within and between island cultural groups and coastal PNG villages, either as single stalks or bundles, with the leaves attached (Haddon 1912; Lawrence 1994). It is highly probably that this practice occurs today, although the magnitude of movement is unknown.

Stalks were either eaten or planted quickly upon receipt (Jesse Sagaukaz, Mayor NPA Regional Council, *pers. comm*.). The conventional method of planting involves laying the entire stalk on the ground horizontally and lightly covering it with soil. Leaves may or may not be present. Alternatively, individual stalks are cut into smaller pieces, generally with the terminal section containing intact leaves, with each section planted base down (Fig. 2-1).

The cultural practice of moving and planting cane with terminal leaves attached (Fig. 2-1) is suspected to be an important way that *E. flavipes* is introduced into novel, or reintroduced into already infested sites within the TS/NPA (Plant Health Australia

2004). This is because *E. flavipes* adults and nymphs are almost always found within the protective spindle-roll leaf cluster of the sugarcane stalk. For mobile life stages to colonise a new area, they must firstly be able to survive several days' transportation on cut stalks of sugarcane, and secondly, either be able to breed on the stalk at the end of a journey or disperse onto nearby established cane plants.

Figure 2-2. Sugarcane planted as sections, with the terminal section (third from left) complete with leaves.

In this chapter, numbers of actively mobile life stages of *E. flavipes* which could survive a long range transportation event, and thus potentially available to colonise a new area, are determined. By confirming this, human-mediated movement of *E. flavipes* via the transport of infested sugarcane stalks becomes a plausible dispersal mechanism for this pest species.

2.2 METHODS

Due to the restricted Australian distribution of *E. flavipes* and associated quarantine issues, the field experiment was conducted at the communities of Bamaga

($10^0$53'S, $142^0$23'E) and New Mapoon ($10^0$52'S, $142^0$23'E), both of which are located on the NPA. A large cultured patch of *S. officinarum* 'java' containing a good breeding population of *E. flavipes* was sourced from New Mapoon. From this, ten stalks infested with *E. flavipes* were selected and cut at the first visible dewlap (the highest unfurled leaf). All of the leaves present on the cut section were collected intact. Stalks were bagged individually in fine meshed polyester gauze bags 1.2 m long and 0.5 m wide to encapsulate the stalks and the *E. flavipes*. Bagged stalks were then transported approximately 3 km by car to Bamaga.

Prior to the introduction of the outboard motor, trading occurred throughout the Torres Strait via large single or double-outrigger sailing canoes (Moore 1978). A six day travelling period would almost certainly see a canoe travel from the PNG coast and reach the southern Torres Strait islands and mainland Australia, an approximate distance of 200 km. To simulate such a transportation event and determine the survival of mobile life stages of *E. flavipes*, each of the ten individually bagged stalks were placed in the shade and left for six days. The numbers of nymphs, males and females migrating off the stalks were counted daily over these six days. Only those insects which were definitely off the leaves and stalk were considered as having deserted, and were thus counted. At the end of six days, the numbers of nymphs, males and females alive or dead *in-situ* on the stalks were counted. The initial starting population was calculated by adding the total population remaining on the stalk to the number of daily deserters. To ensure all remaining insects were counted after six days, each leaf on the stalk was removed and unfurled: this method would have proved too destructive had it been carried out initially. As there was a mixture of live and dead insects on the stalk after six days, the end surviving population was calculated by subtracting the daily deserters and those which were dead on the stalks at the end, from the initial starting population. Each adult was examined for wing-dimorphism. Observations on the condition of the leaves on the cut stalks were also made over the six days.

All statistical analyses and procedures were conducted using SPSS 13.0 for Windows statistical program (SPSS Inc. 2004). All data were tested for normality using the Shapiro-Wilk W test. Statistical comparisons were achieved using ANOVA unless otherwise stated. All significance was set to $P < 0.05$.

2.3 RESULTS

There was a highly significant linear relationship between the mean cumulative number of adults leaving cut sugarcane stalks and the time since stalks were cut (ANCOVA, $F_{1,8} = 468.102$, $R^2 = 0.983$, $P < 0.001$) (Fig. 2-3). There was no difference between the mean cumulative numbers of males and females leaving the stalk (ANCOVA, $F_{1,8} = 0.830$, $P = 0.389$), nor was there an interaction between sex and time (ANCOVA, $F_{1,8} = 3.615$, $P = 0.094$). The mean cumulative number of adults leaving increased, such that over six days both males and females deserted individual stalks at a constant rate of approximately three individuals of each sex per day. In contrast to adults, an exponential relationship better explained the pattern of nymphal desertion of stalks over time ($F_{1,4} = 69.037$, $R^2 = 0.945$, $P = 0.001$) (Fig. 2-3). Nymphs appeared to desert slowly up to day three, at which point the mean cumulative number of nymphs leaving greatly increased with time.

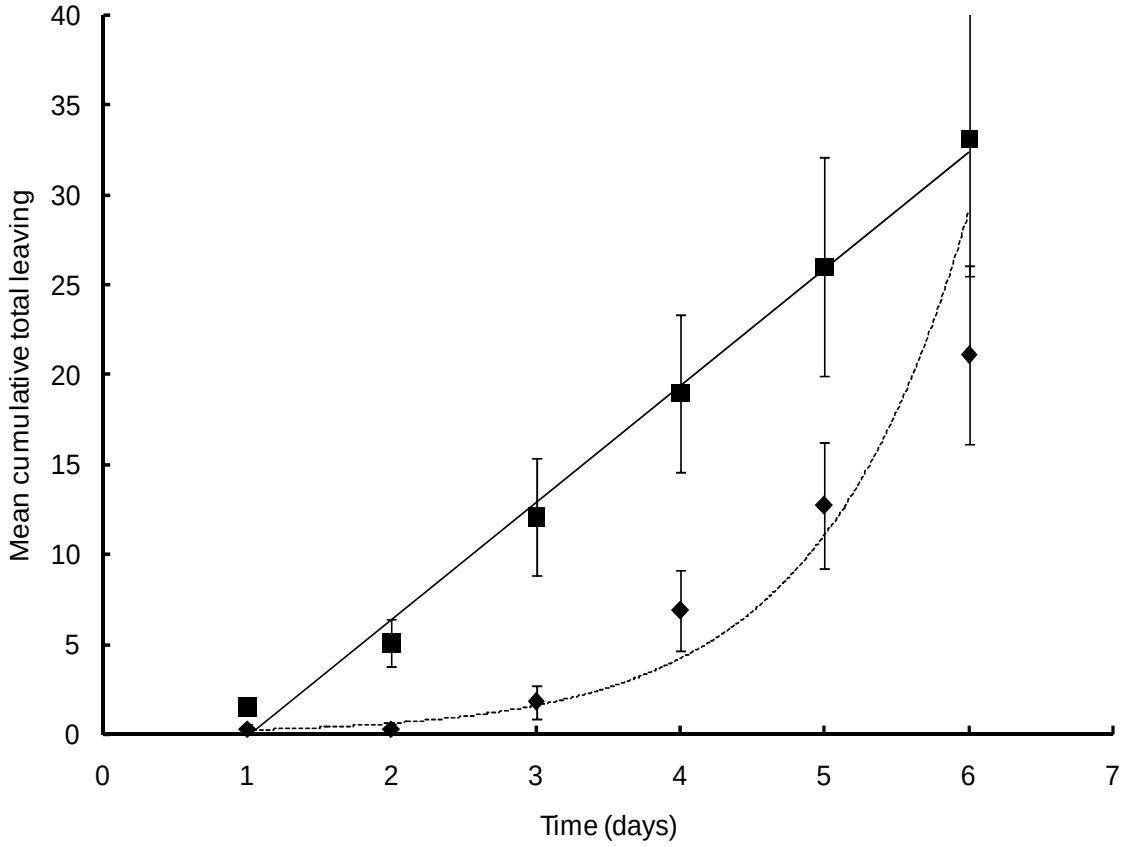


Figure 2-3. The relationship between time since the stalk was cut and the mean cumulative total *E. flavipes* adults (——■——) and nymphs (···◆···) leaving sugarcane stalks over time (2 SE).

There was a significantly larger total number of individuals in the initial population than in the population surviving after six days ($F_{1,2}$ = 60.431, P = 0.016). A significantly higher proportion of nymphs survived than adults, but there was no difference between the numbers of surviving adult males and females ($F_{2,2}$ = 33.191, P = 0.029). Of the initial nymph population, 48 % (± 1.3) were left alive in the spindle roll after six days. A similar proportion of the initial population of males and females survived on the stalk for six days; this being 26 % (± 0.7) and 27% (± 0.8) respectively (Fig. 2-4). There was no interaction between life-stage and numbers surviving ($F_{2,54}$ = 0.557, P = 0.576).

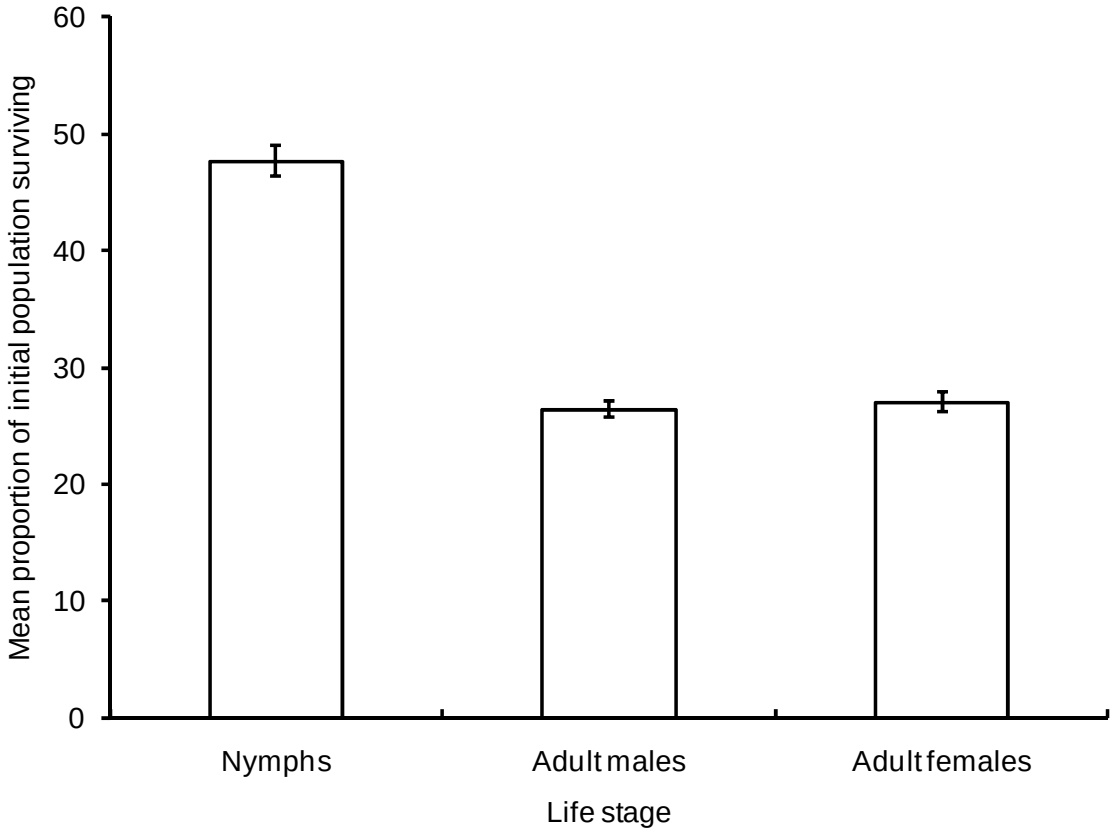


Figure 2-4. Proportion of the initial population of *E. flavipes* nymphs, adult males and adult females alive per stalk after six days on cut sugarcane (2 SE).

All of the adults (n = 508) counted had wings which extended beyond the abdomen. No adults exhibited obvious reduced meso- or metathoracic wings that may have indicated the presence of a flightless form. At the end of day six, the only entirely

green tissue present on the sugarcane stalks was on the inner leaf of the spindle roll and at the base of the inner leaves. All of the outer leaves were brown and appeared very dry, probably indicating major water loss from the stalks.

2.4 DISCUSSION

Insects possess an innate ability to escape deteriorating host plants to find others which are more optimal, especially if the insect and its host plant have co-evolved (McClure 1983). *E. flavipes* is thought to have evolved on sugarcane in PNG (see chapter four) and may thus be able to quickly detect changes in sugarcane host quality. Visual observations made during the course of the experiment indicated that the cut sugarcane stalks were drying, and wilting is known to prompt dispersal in leafhoppers (Waloff & MacFadyen 1980). Planted sugarcane ceases to grow five days after irrigation has stopped (Ham *et al.* 2000). A cut stalk would be expected to deteriorate quicker than an intact plant starved of water, as there is no soil moisture available to the cut stalk. That adults began dispersing from stalks within a day of cutting likely indicates a fast response to some aspect of host deterioration.

Whether any individuals are left on a stalk to colonise following transportation will be dependent upon the starting population size. Numbers of individuals per stalk varies greatly throughout the TS/NPA, and may range from zero individuals to 'hot-spots' of infestation, where plants may harbour as many as 279 individuals on a single stalk. However, when infested, the average TS/NPA infestation per stalk is 32.7 nymphs and 3.99 adults (calculated from data collected during 2006, for chapter four). A 'banana boat with a 40 – 60 hp outboard motor travels from the PNG area around Saibai, Boigu or Dauan to the mainland in about four to five hours, but you can do it much quicker in a speed-boat' (Jackson Sailor, Australian Quarantine and Inspection Service - Bamaga, *pers. comm.*). Given the average TS/NPA stalk infestation, a one day travel period through the TS in a boat would be ample time to reach any number of destinations throughout the region, with the majority of the starting population still *in-situ* on the stalk.

As the number of arriving colonists at any one time is known to be proportional to colonisation success (Drake & Lodge 2006), it is possible that the small remaining

proportion of adults surviving *in-situ* on a stalk toward the end of six days may decrease the likelihood of colonisation. A small colonising population decreases the propagule pressure, or availability of colonists, but there may be as yet unknown characteristics of *E. flavipes* ecology and life-history that serve to negate these effects following immigration (Lawton & Brown 1986; Williamson & Fitter 1996; Denno *et al.* 2008). For example, if sugarcane was particularly abundant on the destination island, then the *E. flavipes* dispersing from stalks that had just been delivered, especially if it was a short trip, may be more likely to locate suitable host and potentially colonise to form large populations (Lawton & Schroder 1977). Generally, host-specific insects such as *E. flavipes* are considered to have a high searching ability to allow the discovery of even rare hosts (Debach 1965), and host abundance is known to increase the potential for successful colonisation (Worner 2002). This scenario may be more likely on Torres Strait islands such as Boigu, Saibai and Mer, where sugarcane is grown abundantly in many gardens, or where there are large patches of wild sugarcane, such as Ngurupai.

Similarly, the presence of similar numbers of males and females may offset any negative effect of a small introductory population because mate location in a new habitat may prove very efficient. Mate calling by males occurs immediately upon settlement on a host plant (Denno 1994b). This 'fly and call' strategy appears to be particularly successful under low density conditions for locating virgin females that are newly arrived (Denno & Roderick 1990). Generally, migratory female planthoppers are not mated and will search for a mate upon arrival in a new habitat (Denno 1993).

Interestingly, nymphs responded more slowly than adults to deteriorating host quality and remained on the cut stalks until day three, when they left at a faster rate. Nearly half of the initial population of nymphs survived the six day treatment, so if colonisation conditions were satisfied, nymphs may also possess the capability to colonise a new area. Nymphal *E. flavipes* tend not to leave a sugarcane plant unless disturbed, but it was observed that if knocked from a stalk, they could easily move several metres by running sideways, backwards or hopping. *Perkinsiella saccharicida* Kirkaldy nymphs exhibit similar movements, and if knocked off are able to disperse a metre or two from the host cane or return to the host cane within a few hours (Pemberton 1949). If a transported stalk was planted in a patch which already contained established sugarcane plants onto which the nymphs could walk, feed and develop into adults, it is likely that this would lead to a successful colonisation event.

The adults of many species of planthoppers exhibit extreme wing dimorphism (Denno 1994b). Macropters are fully winged individuals capable of long-distance migratory flight, whilst brachypters are flightless due to varying degrees of wing reduction (Denno 1994b). Brachypters disperse by hopping or walking, and their movement is generally limited to within 10 metres of their host plant (May 1975). Not one of the adults inspected during this study exhibited any marked reduction in wing length, implying that every individual is capable of flight. However, in some species of planthopper, a sub-macropterous form may also exist, where flight capability is limited due to partially reduced wings (Waloff & MacFadyen 1980). Sub-macropterous forms probably do not disperse via flight but can disperse short distances via walking or hopping (Denno 1994b). Certainly it was noted that some *E. flavipes* individuals did not fly when disturbed, but instead ran sideways, whereas others did engage in flight of a few metres. Further research is required to reveal the presence of a sub-macropterous form in the island sugarcane planthopper.

Results of this chapter clearly demonstrate that *E. flavipes* individuals are able to survive for up to six days on a cut stalk of sugarcane, which is ample time for movement across the entire Torres Strait. Although the magnitude of such movement is unknown, anthropogenic movement may be highly important in facilitating the movement of *E. flavipes* throughout the Torres Strait.

CHAPTER 3 WIND-ASSISTED IMMIGRATION POTENTIAL

Publication Arising:

Anderson, K.L., Deveson, E.D., Sallam, M. & Congdon, B.C. 2010. Wind-assisted migration potential of the island sugarcane planthopper, *Eumetopina flavipes* (Hemiptera: Delphacidae): implications for managing incursions across an Australian quarantine frontline. *Journal of Applied Ecology,* **47,** 1310-1319 (IF = 4.2, ERA = A)

3.1 INTRODUCTION

Annual, north-westerly monsoonal trade winds may promote dispersal of exotic organisms through the Torres Strait (Farrow & Drake 1978; Farrow *et al.* 2001). Unlike other transport mechanisms, wind provides the perfect opportunity for a 'continuing rain of propagules' from PNG into the TS/NPA, a process that could enhance the survival of exotic species in the region (Thresh *et al.* 1983; Simberloff 2009). In general, planthoppers rely on wind for migrations over significant distances (Kisimoto & Rosenberg 1994). Consequently, wind-assisted, long-distance migration from PNG may explain, at least in part, the distribution and extinction/recolonisation dynamics of *E. flavipes* in the TS/NPA.

The likelihood and relative magnitude of long-distance, wind-assisted migration can be determined using trajectory analyses that incorporate meteorological data and ecological parameters for the organism of interest (Reynolds *et al.* 1997). In this chapter, such analyses were used to determine if wind-assisted migration of *E. flavipes* from PNG into the TS/NPA and beyond is possible, and to gain an insight into its potential frequency and the likely resulting distribution.

3.2 MATERIALS AND METHODS

3.2.1 *The long-distance migration model*

The long-distance migration model used in this study was developed to predict the change in distribution of *Helicoverpa* moths following a migration event (Rochester *et al.* 1996). Fallout regions have been accurately predicted by the model for a variety of noctuid moths (Gregg *et al.* 2001). The model has since been used to show that winds between 100 – 400 m altitude were sufficient to transport mosquitoes from PNG into the TS and onto mainland Australia during the monsoon season (Ritchie & Rochester 2001), as well as to predict trajectories for identifying the direction and distance of locust migrations in Australia (Deveson *et al.* 2005).

The long-distance migration model uses a number of sub-models to calculate a resulting distribution following a period of migration, in the following manner (from Rochester *et al.* 1996). First, a representative, random sample of 'insects' is generated by selecting their location from a source population defined by the user. Then, each insect is flown along its trajectory, which is determined by the wind velocities around it and its responses to environmental conditions experienced during the flight. The responses are randomly selected from a set of possible responses (the range of which is specified by the user), which can change during the flight. The end point of each trajectory is accumulated and passed to the result population distribution sub-model, and once the result distribution remains constant, the final numbers and distribution of insects is calculated. When the sub-model parameters are random variables, their values are randomly selected from a uniform probability distribution using the Generic Spatial Insect Model (GenSIM) random variates generator. The assignment of arbitrary distributions to the random model parameters enables the model to be flexible as it examines various behavioural influences on long-distance migration (Rochester *et al.* 1996). In doing this, the full range of parameter values and their impact on flight is examined during the simulations, and is thus reflected in the resulting distribution.

3.2.2 *Source population*

E. flavipes source population was defined as an area of roughly 2, 500 km^2, extending approximately 260 km along the southern coast of PNG and 100 km inland

from the PNG coast, with the Fly River forming the north-eastern boundary, and the border between PNG and West Papua forming the western boundary (Fig. 3-4). The environment is mainly lowland alluvial plains and fans, and freshwater swamps (Paijmans 1976), and contains an abundance of *E. flavipes* 'wild' host plants, these being *Saccharum robustum* Brandes & Jeswiet ex Grassl and *S. spontaneum* L., which form pure stands in suitable habitat (Paijmans 1976). As well, *E. flavipes* has been sampled on the highly favoured hosts *S. edule* Hassk., *S. officinarum* L. and *S.* 'hybrids' in local village gardens and surrounds (Magarey *et al.* 2002).

The source population is represented as a grid in the model, and the distribution of insects within the source population is based on the number of insects within each grid square (Rochester *et al.* 1996). The starting location of each insect inside each grid square is randomly generated (Rochester *et al.* 1996). In this study, the source population contained 250 x 10 km^2 grid squares, and we nominated 40 insects per 10 km^2 grid square, giving a total 10, 000 individuals migrating on each date. The size of the source population was used as an index of the relative density of possible migrants. In light of recently published data which shows *E. flavipes* abundance in PNG may be as high as 201 adults per plant (Chapter four; Anderson 2009), the specified 40 insects per 10 km^2 may be a highly conservative estimate, especially in areas of high host abundance.

3.2.3 ***Flight parameters***

A number of parameters are required by the model in order to calculate flight direction and distance during the simulations. Virtually nothing is known about *E. flavipes* migratory capacity, but migratory flight behaviour is well documented for a range of other planthopper species. In keeping with the majority of migratory take-offs by planthoppers in tropical regions occurring at dusk (Padgham *et al.* 1987), *E. flavipes* has been observed to move to the stalk tips of commercial sugarcane at Ramu Agri-Industries, PNG, at dusk (K. Korowi, Ramu Agri-Industries Ltd., *pers. comm.*). For this reason the take-off time specified in the model was 18.30 AEST. The flight bearing offset angle required by the model allows the simulated flying insects to 'control' the direction of flight. In nature, many insects are capable of this, particularly when correcting for crosswind drift (Dingle 1996; Chapman *et al.* 2008). However, planthoppers are known to migrate at altitudes where the wind speed exceeds their flight

speed, so their flight displacement is primarily a function of wind direction and speed (Kisimoto & Rosenberg 1994; Riley *et al.* 1994). The offset angle specified in this study thus allows for nil to minor control over flight direction during simulations. In the absence of data for *E. flavipes*, the remaining parameters were based on ranges published for *Nilaparvata lugens* Stål and *Sogatella furcifera* (Horvath) (Ohkubo 1973; Seino *et al.* 1987; Watanabe & Seino 1991; Kisimoto & Rosenberg 1994) (Table 3-1).

Table 3-1. List of estimated *E. flavipes* flight parameters

Parameter	Minimum	Maximum
Flight bearing offset angle (degrees)	45	-45
Flight speed (metres per second)	0	2
Flight duration (hours)	1	24
Flight altitude (metres)	100	1000

3.2.4 ***Simulations***

The wind sub-model uses outputs from the limited area prediction system (LAPS) regional atmospheric circulation model run by the Australian Bureau of Meteorology (BOM) (Puri *et al.* 1998), and was first used to generate wind trajectories for each 24 hour period between 1 January 2003 to 31 December 2007, from three PNG locations, being Morehead (inland PNG) $8^0$37’37”S $141^0$38’19”E, Buji (Coastal PNG) $9^0$09’05”S $142^0$14’17”E, and Daru (Coastal PNG) $9^0$04’42”S $143^0$12’36”E. The three locations lie in the north-west, north-east and south of the source population area, respectively. Each 24 hour wind trajectory projection was saved as a graphics file, and visually assessed. For each 24 hour projection, if any of the wind trajectories ran from the PNG source population into the TS/NPA, the full model which incorporated insect flight parameters was run for that date, and the resulting distribution of immigrants calculated at 21 TS/NPA locations (Table 3-2). Alternatively, if all wind trajectories ran in a northerly direction away from the source population, nil immigration into the TS/NPA was recorded and the full model was not run. Trajectory simulations were not possible for several nights in July 2005 or 15 February 2006, because LAPS outputs were unavailable.

Table 3-2. Torres Strait island and northern peninsula area locations sampled for predicted numbers of *E. flavipes* from resulting distribution.

Traditional group	Location	GPS Co-ordinates
NPA	Bamaga	$10^0$53’38.13”S 142^{0}23’20.76”E
	New Mapoon	$10^0$52’01.38”S 142^{0}23’08.05”E
	Injinoo	$10^0$54’32.13”S 142^{0}19’24.57”E
Inner	Muralug	$10^0$36’33.57”S 142^{0}12’34.81”E
	Ngurupai	$10^0$35’34.89”S 142^{0}14’53.99”E
	Waiben	$10^0$34’55.79”S 142^{0}13’19.49”E
	Keriri	$10^0$33’18.37”S 142^{0}13’10.20”E
Western	Moa - Kubin	$10^0$14’02.02”S 142^{0}13’14.27”E
	Moa - St Pauls	$10^0$11’06.68”S 142^{0}19’42.79”E
	Badu	$10^0$09’01.17”S 142^{0}10’12.25”E
	Mabuiag	$9^0$57’25.26”S 142^{0}11’13.88”E
Top Western	Boigu	$9^0$13’50.34”S 142^{0}13’11.80”E
	Dauan	$9^0$25’08.35”S 142^{0}32’29.76”E
	Saibai	$9^0$22’54.16”S 142^{0}36’42.39”E
Eastern	Ugar	$9^0$30’27.72”S 143^{0}32’49.06”E
	Erub	$9^0$35’08.24”S 143^{0}46’14.67”E
	Mer	$9^0$54’53.91”S 144^{0}02’29.55”E
Central	Masig	$9^0$45’01.82”S 143^{0}24’46.84”E
	Iama	$9^0$53’54.93”S 142^{0}46’06.97”E
	Poruma	$10^0$03’00.23”S 143^{0}03’54.22”E
	Warraber	$10^0$12’16.69”S 142^{0}49’24.35”E

3.2.5 ***Data analysis***

Differences in predicted patterns of seasonal long-distance, wind-assisted migration from PNG into the TS/NPA were investigated by examining variation in monthly predicted immigration using non-parametric Kruskal-Wallis. This technique was used due to non-normality of the dataset (Quinn & Keough 2006).

The simulated TS/NPA spatial distribution was examined to determine whether certain TS/NPA locations or island/community groups were at greater risk of

immigration than others. First, the frequency of immigration events was examined. If > 0 immigrants were observed within a location or island/community group on a particular day, then it was classified as a 'hit', whereas zero immigrants were a 'miss'. The frequency of hits and misses for each TS/NPA location and group were compared using a two-way contingency table analysis, and associated Pearson χ^2 statistic (Quinn & Keough 2006). Location data were natural logarithm transformed to correct non-normality (Quinn & Keough 2006), and ANOVA and LSD *post-hoc* tests used to detect any significant difference in the numbers of predicted immigrants per hit day between locations. The Welch correction and Tamhane's *post-hoc* tests were used for the group ANOVA due to unequal variance (Quinn & Keough 2006).

E. flavipes simulated spatial distribution and abundance was compared to observed infestation at different TS/NPA locations; the latter were calculated using mean *E. flavipes* abundance per TS/NPA location over time (Chapter four; Anderson *et al.* 2009 for detailed field sampling methodology). Time constraints at some sampling locations in 2006 meant that all host plants were not sampled as they were in 2008. To account for the differential sampling effort between years, *E. flavipes* 2006 infestation was adjusted to reflect the infestation expected for the total number of host plants present in that year (H_1), which was calculated as $H_1 = N_1 / (t_1 / t_2)$, where N_1 is the number of plants sampled in 2006, t_1 is the hours spent sampling in 2006, and t_2 is the hours spent sampling in 2008. To determine whether simulated patterns of wind-assisted immigration alone could explain the observed pattern of infestation, regression analysis was performed on ln (x + 1) transformed data to correct non-normality. In addition, a non-parametric Kendall's tau test was used to determine if any other relationship existed between predicted immigration and observed infestation (Quinn & Keough 2006).

A wide array of stochastic processes may affect establishment following immigration (Williamson 1996; Lockwood *et al.* 2007). It is not known what these might be for *E. flavipes*. For this reason, three different establishment probabilities (100 %, 30 % and 10 %) were used to account for these factors in comparisons between simulated immigration and observed infestation rates. This also effectively examines the changes that would occur as a result of varying source population (propagule) size during the modelling procedure.

3.3 RESULTS

3.3.1 *Annual patterns in the TS/NPA*

No immigration was predicted from PNG into the TS/NPA from June through to October. For November to May, the mean total predicted number of immigrants varied significantly between months (χ^2 = 19.96, d.f. = 6, P < 0.01; Fig. 3-1). Immigration in November occurred in only two of the five study years, with November experiencing the lowest rates of all months in which immigration occurred. The highest immigration was consistently predicted to occur during January, February and March, with average rates between approximately 4000 and 7000 individuals. Predicted numbers of immigrants did not differ significantly between these three months between years (χ^2 = 3.140, d.f. = 2, P = 0.21). During December, April and May, simulated immigration rates were lower, but varied considerably more between years. In December, highly variable numbers of immigrants occurred every year during the study (between 24 and 5000), while in April, immigrants occurred in only three of the five years and numbers were highly variable (between 0 and 7455). Only in 2006 were immigrants predicted in May.

The results suggest that for *E. flavipes*, the migratory season begins in December, or occasionally late November, but that the exact initiation date varies from year to year. The migratory season usually ends in March, but in some years it can continue until April. Very rarely does the season end in May, as it did in 2006. However, in that year severe tropical cyclone 'Monica' traversed Cape York Peninsula and the Northern Territory of Australia from mid to late April. This resulted in strong winds from PNG into the TS/NPA persisting until early May, the only year during the study when they did so. This finding clearly suggests that extreme weather events can increase variation in the number of immigrants reaching the TS/NPA and lengthen the migratory season for up to one and a half to two months beyond likely long-term averages.

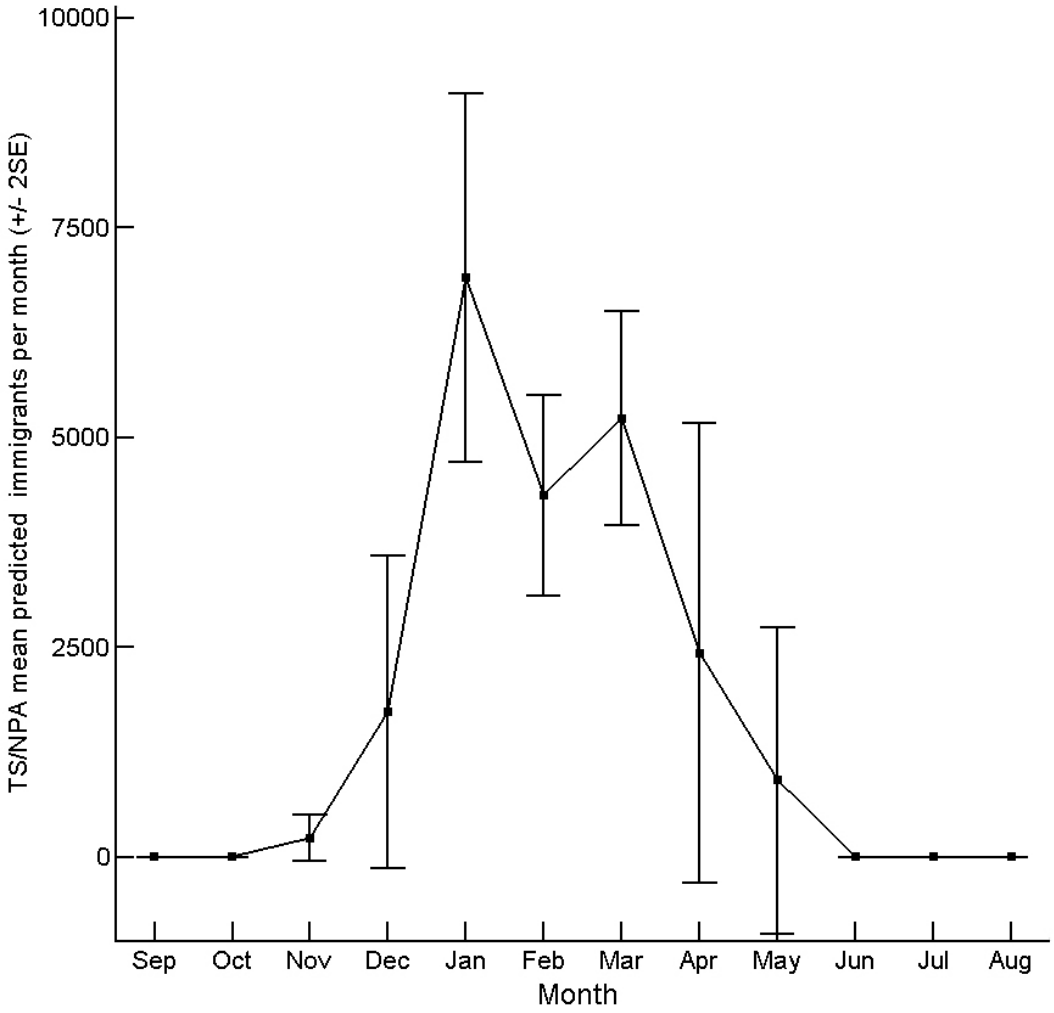


Figure 3-1. Mean number of predicted *E. flavipes* immigrants per month (2 SE) throughout the Torres Strait and northern peninsula area, Cape York, Australia, from January 2003 to December 2007.

3.3.2 ***Simulated spatial patterns in the TS/NPA***

Wind-assisted migration from the theoretical PNG source population to all sampled locations in the TS/NPA appears possible. Importantly, it was noted during visual assessment of the 24 hour wind trajectory projections, that some trajectories from PNG end south of Cairns, which is a major commercial sugarcane production area, as occurred on 12 March 2003 (Fig. 3-2). In response to this result, BOM Mean Sea Level Pressure (MSLP) weather charts were examined for i) 12 March 2003 at 4 pm and 10 pm AEST, ii) 4 am, 10 am and 4 pm on the 13 March 2003, and iii) for the 20

days during the study period where every TS/NPA location was predicted to receive immigrants. A number of synoptic scenarios appear to be responsible.

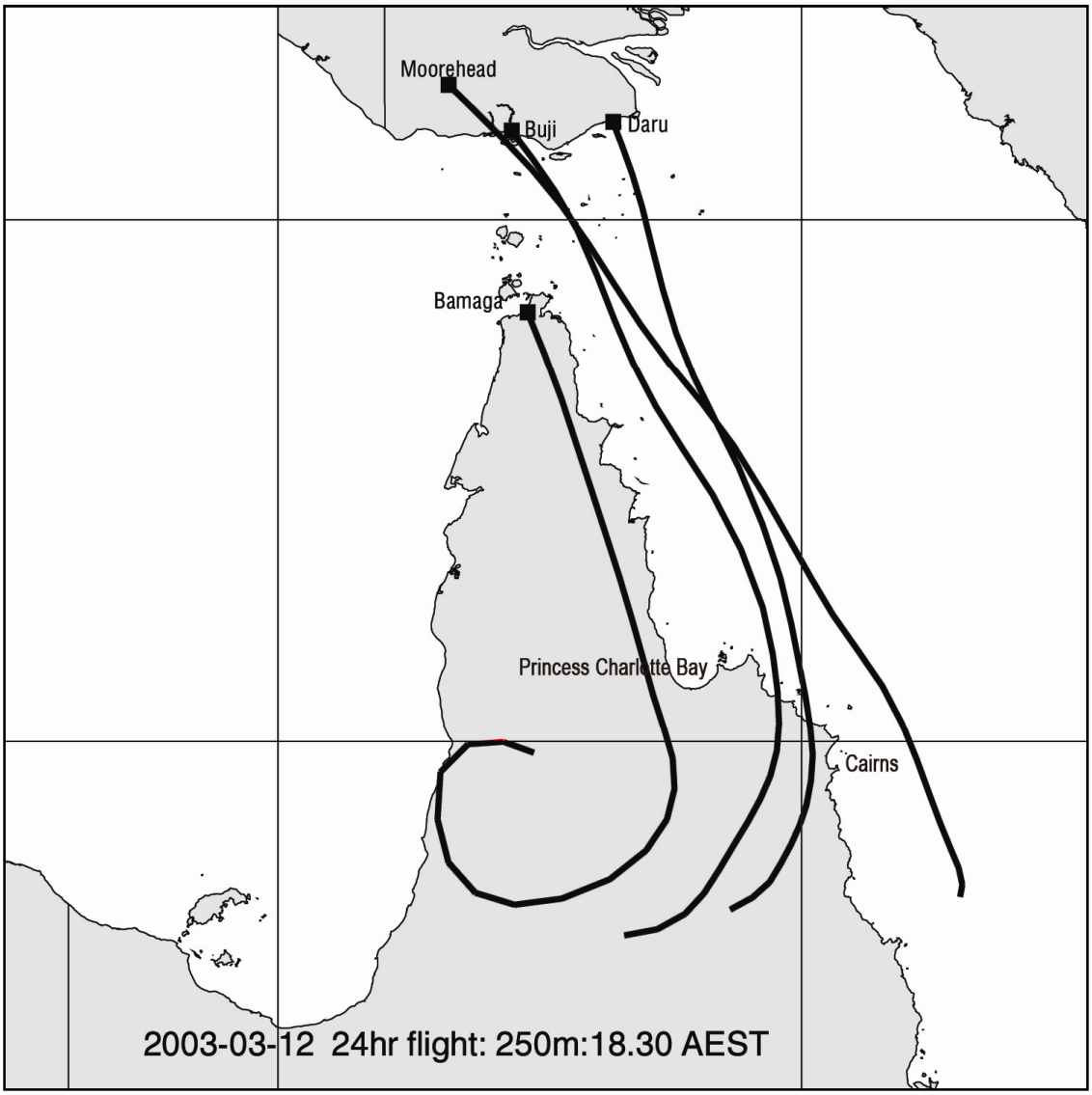


Figure 3-2. Model simulation of *E. flavipes* trajectories from Morehead, Buji and Daru, Papua New Guinea, and Bamaga, northern peninsula area, Queensland, for a 24 hour flight from 18.30 AEST on 12 March, 2003 where the modelled trajectories end south of Cairns, Australia.

On the 12 March 2003, tropical cyclone 'Craig' was present in the Gulf of Carpentaria but was downgraded to a tropical low as it crossed over the southern area of Cape York. Therefore, very long southward trajectories appear to be associated with a depression or cyclone present further south over Cape York. In general, blanket immigration throughout the TS/NPA is associated with either i) a low pressure system or a tropical cyclone in the Gulf of Carpentaria, ii) a low over the tip of Cape York

Peninsula which produces similar southward movement but over shorter distances, and iii) a more complex situation with lows to the west and east with a 'trough line' running across top of Cape York Peninsula or through the TS.

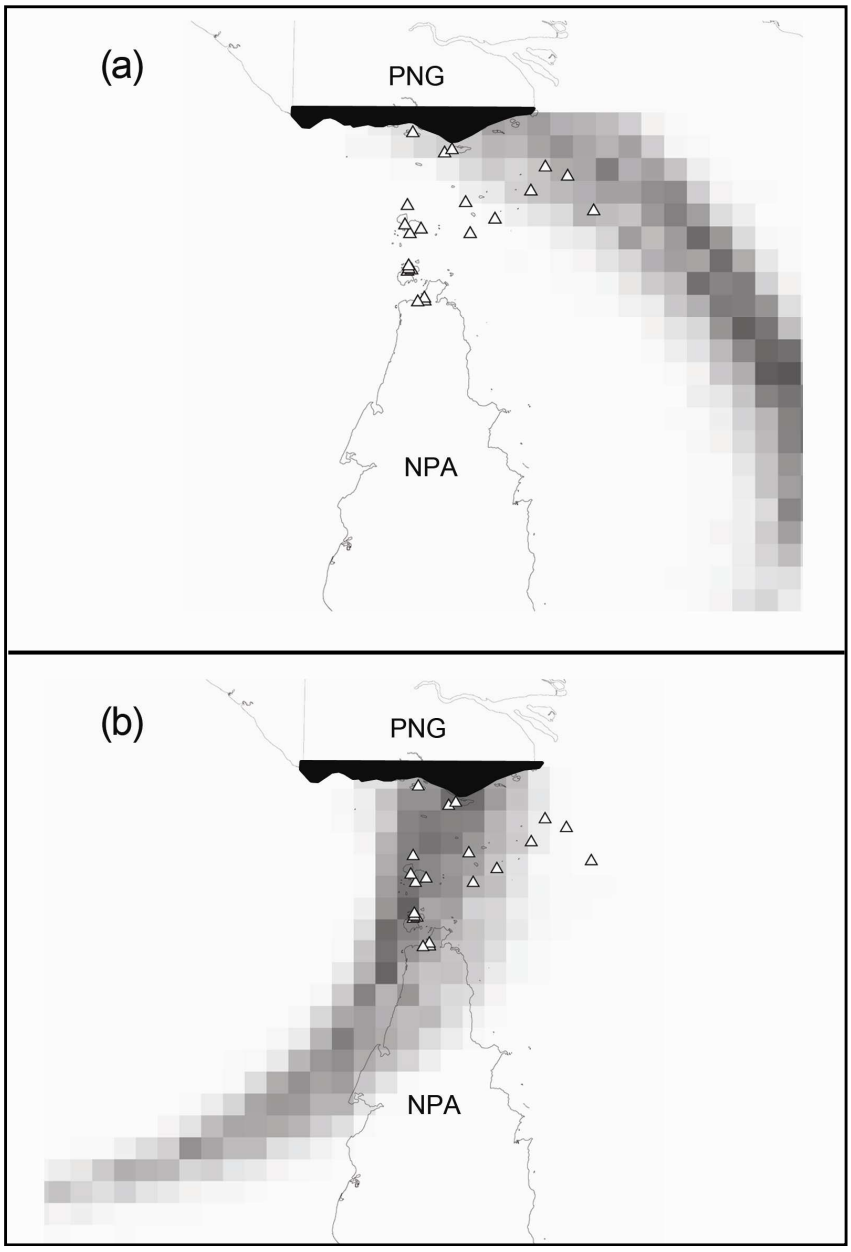


Figure 3-3. *E. flavipes* simulated migration from theoretical Papua New Guinea (PNG) source population (black shaded area) to the Torres Strait island and northern peninsula area (NPA) of Cape York, Australia (Δ sampling locations), for (a) 12 February, 2004, and (b) 11 March, 2005. Light grey to dark grey squares indicates a low to high abundance, respectively, of potential immigrating *E. flavipes*.

The proportion of hits differed significantly between TS/NPA locations (χ^2 = 2261.50, d.f. = 20, $P < 0.001$) and island/community groups (χ^2 = 2138.47, d.f. = 5, $P < 0.001$). This is because not every TS/NPA location or group sampled was hit with immigrants on each day. For example, most Central group locations as well as all Top Western and Eastern group locations were hit on 12 February 2004 (Fig. 3-3a), whilst on the 11 March 2005, all locations except Mer were hit (Fig. 3-3b).

For hit days only, the mean ln (predicted number of immigrants per year) differed significantly between TS/NPA island/community groups ($F_{5,\ 44.71}$ = 120.88, $P < 0.001$; Fig. 3-4). The Top Western group was predicted to receive the most immigrants per year of all groups, followed by the Eastern, then the Central groups (Tamhane *post-hoc* tests). The NPA, Inner and Western groups received the fewest immigrants, with numbers of immigrants being relatively similar (Tamhane *post-hoc*: NPA and Inner, P = 0.612; Inner and Western, P = 0.193; NPA and Western, P = 0.045; Fig. 3-4).

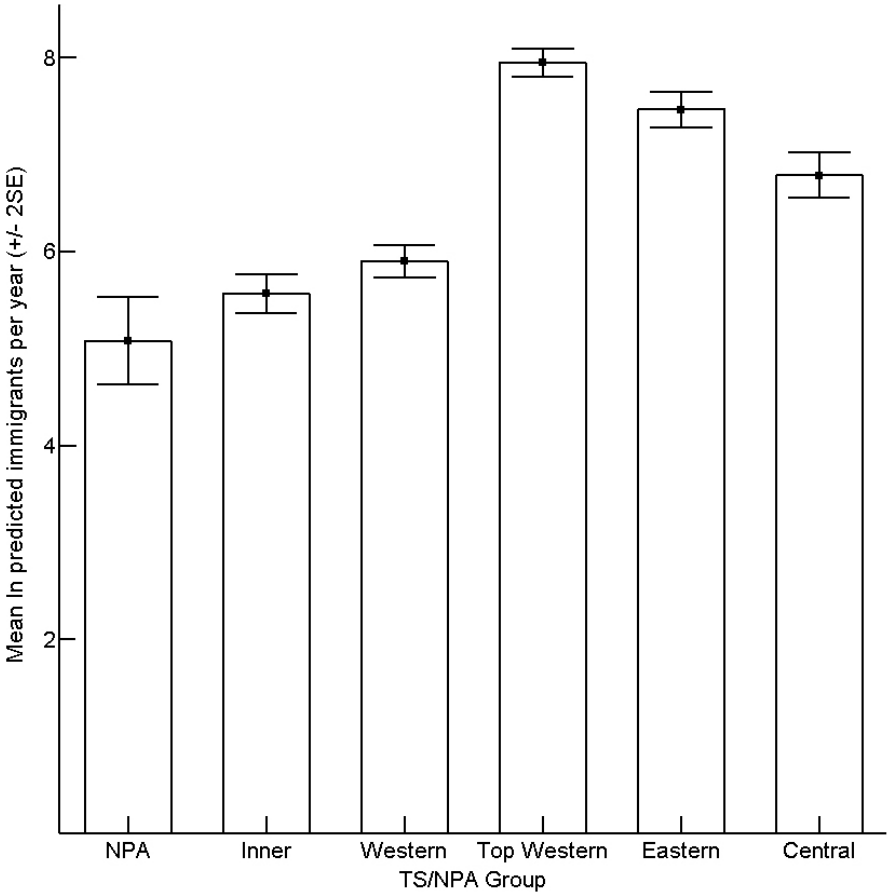


Figure 3-4. Mean number of predicted *E. flavipes* immigrants per year (2 SE) by Torres Strait island and northern peninsula area of Queensland, Australia, traditional island/community group.

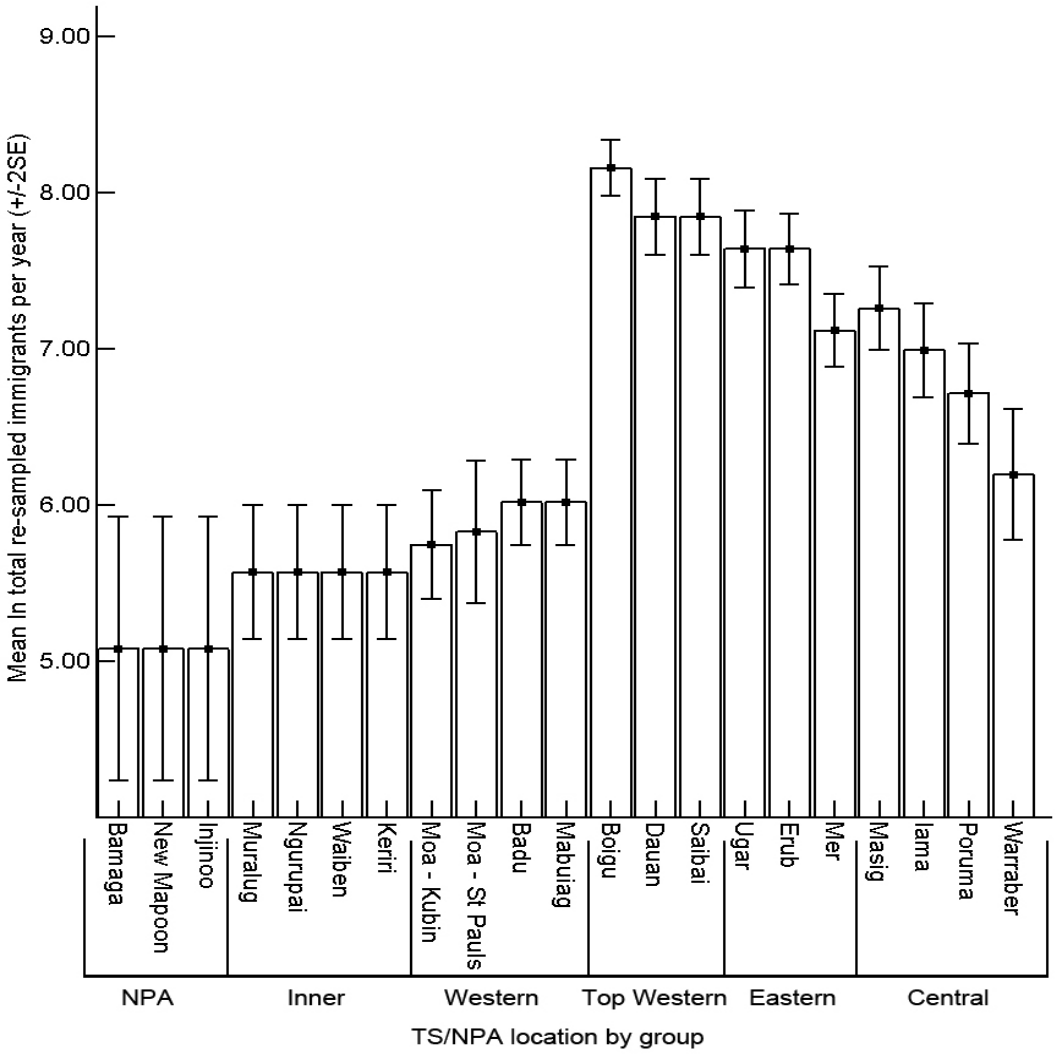


Figure 3-5. Mean number of predicted *E. flavipes* immigrants per year (2 SE) by Torres Strait island and northern peninsula area of Queensland, Australia, traditional island/community group.

3.3.3 ***Simulated versus observed infestation***

There was no significant linear ($F_{1,\ 20}$ = 0.50, Adj R^2 = -0.025, P = 0.49) or monotonic (correlation coefficient = 0.12, P = 0.46, n = 21) relationship between the mean predicted immigration and the mean observed infestation per TS/NPA location (Fig. 3-6). Therefore, in general, the number of immigrants predicted to reach each location per year due to wind-aided migration alone does not match observed patterns of *E. flavipes* infestation throughout the TS/NPA.

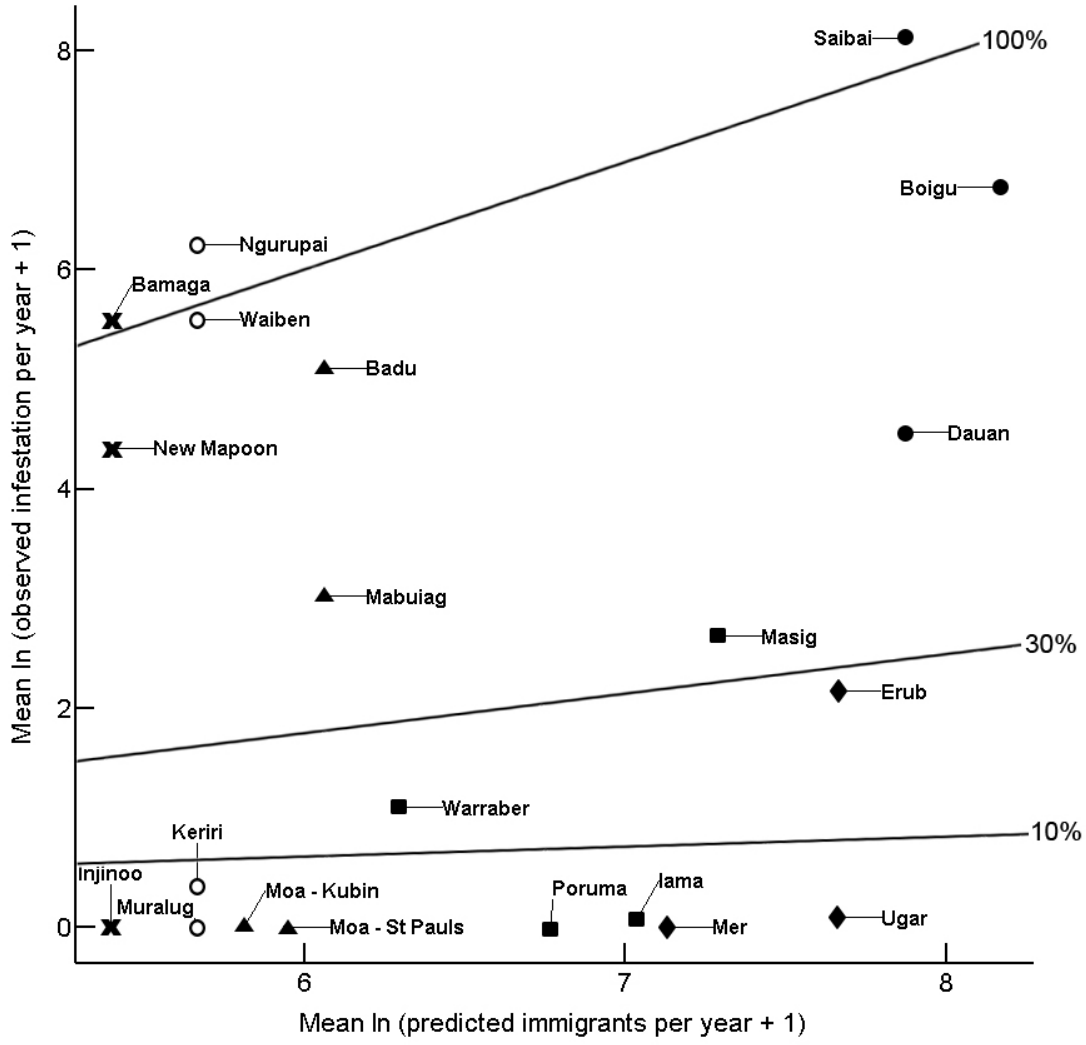


Figure 3-6. Relationship between the mean number of predicted *E. flavipes* immigrants per year and the mean observed *E. flavipes* infestation per year for all TS/NPA locations. Lines represent the theoretical expected infestation should 100 %, 30 % or 10 % of the mean number of predicted immigrants establish (traditional island/community group symbols: NPA **X**, Inner ○, Western ▲, Central ■ , Top Western●, Eastern⧫).

These data can also be compared to the three hypothetical levels of establishment success. The results suggest that some individual locations may fit the theoretical relationships. For example, the observed infestations at Saibai, Bamaga, Ngurupai and Waiben close to the line of 100 % of immigrants colonising (Fig. 3-6). Infestations at Masig and Erub appear consistent with 30 % of the predicted immigrants successfully establishing (Fig. 3-6). However, there does not appear to be a general level of

establishment success that would allow the numbers predicted to match observed infestation throughout the TS/NPA. Similarly, within island/community group, there does not appear to be a general level of establishment success where the predicted numbers of immigration match the observed infestation. For example, the predicted immigration to all locations within the NPA group is identical, but the observed infestation is highly variable; a pattern repeated across most groups. Importantly, there are a number of locations in the TS/NPA with no infestation at all, despite relatively high rates of predicted immigration.

3.4 DISCUSSION

Simulation results strongly suggest that wind provides multiple opportunities for *E. flavipes* to immigrate from PNG into the TS/NPA. Although based on general planthopper flight behaviour, this result could be true for any organism that migrates with wind assistance. Simulations predict that immigration should begin in late November or December, peak between January and March, and rarely continue past April. This finding is consistent with the frequently observed movement of large numbers of different insect taxa from PNG into the TS during the monsoon season (Farrow & Drake 1978). No immigration was predicted from June through to October during the dry season, when circulation is dominated by south-easterly trade winds (Suppiah 1992). Variability in the onset, length and cessation of the monsoon season, including associated summer monsoon winds, is complex and closely linked to cycles that include the Madden-Julian oscillation, El Niño/ Southern oscillation phenomenon and the Quasi-biennial oscillation (Suppiah 1992). The intricate way that these and other cycles interact to cause monsoon onset make it very difficult to develop accurate, predictive models of year-year variation in immigration from PNG. However, analysis of wind direction and strength associated with particular synoptic events may allow risk alerts at appropriate times.

On average, cyclones pass through the TS once every eight or so years (Babbage 1990). This study spanning five years and including one cyclone is thus fairly characteristic of average extreme weather event occurrence. Cyclones are known to affect monsoon onset (Suppiah 1992), so delayed monsoon cessation in April 2006

resulting in a continuation of the immigration season until May of that year, may have been caused by the presence of TC Monica. As a general observation, a depression or cyclone in the Gulf of Carpentaria or over Cape York Peninsula establishes suitable wind conditions to allow for long-distance, widespread immigration from PNG into northern Australia. Such wind conditions were sufficient to carry mosquitoes from PNG to the NPA for 79 % and 57 % of the days during December 1997 and January 1998 respectively (Ritchie & Rochester 2001). Winds on one particular night transported mosquitoes a distance of approximately 678 km (Ritchie & Rochester 2001). For planthoppers, seasonal displacements in Asia are known to occur annually on monsoon winds, particularly those associated with frontal depressions and typhoons (Rosenberg & Magor 1987). The continuous air currents allow long-distance transport from several hundreds to thousands of kilometres away from the source population (Kisimoto 1976; Seino *et al.* 1987). The development of a low pressure system in the Gulf of Carpentaria, at the least, was thought to be essential for insect migration from PNG to Cape York (Farrow & Drake 1978). Results suggest there is potential for *E. flavipes* to easily be transported similar distances without the aid of such systems. However, when low pressure systems are present, not only may they extend the immigration season and potentially promote widespread immigration, they may also potentially transport *E. flavipes* south of the NPA to commercial sugarcane growing regions near Cairns. Of interest is that *E. flavipes* has not been detected south of the NPA. Many factors could be responsible for this anomaly. Perhaps it is only a matter of time, as was the case with the incursion of sugarcane smut into the Ord River Irrigation Area in Western Australia, which was highly suspected to be wind-borne from Indonesia (Croft & Braithwaite 2006).

Even allowing for minor flight control, it appears that prevailing wind conditions and distance from PNG are the dominant processes responsible for the resulting predicted distribution of *E. flavipes*. The Top Western group of islands may have received the greatest number of immigrants because they are close to PNG, and because trajectories over a range of wind directions, from north-west through to south-east, contact islands in the group, particularly Boigu. This finding is consistent with the Top Western islands, of all islands, receiving the greatest numbers of exotic fruit fly species from PNG (Technical Advisory Panel on exotic fruit flies for Plant Health Committee and Primary Industries Standing Committee 2004), and other wind-dispersed organisms like disease-carrying midges and mosquitoes (Johansen *et al.*

2003). The predicted frequency of immigrants per group dwindles as northerly winds become more frequent and/or with greater distance from PNG. Farrow & Drake (1978) suggest that wind trajectories from the Papuan region would rarely reach Cape York, so that a successful southward crossing of the TS was unlikely. In contrast, results suggest that *E. flavipes*, at least, may regularly reach the NPA during the monsoon season, and locations in the Western, Inner and NPA groups, albeit lower than other groups, may still be at risk of annual invasion.

Clearly, uncertainties are an issue in predictive modelling, and error and bias can cause predictions to fail (Regan *et al.* 2002). In this case, the impact of altering some model parameters (for example to reflect natural abundance variation in the source population) may lead only to over or under-estimation of individuals in the resulting distribution, not to a change in the resulting distribution itself. As discussed earlier, the resulting distribution is primarily driven by wind, not arbitrary decisions made during the modelling process. Therefore the predictive power of the model is high, and distributional inferences are unlikely to be incorrect (Johnson & Gillingham 2008).

Overall, results of this chapter suggest a high potential for wide-spread, wind-assisted immigration from PNG into the TS/NPA. There are some locations where wind-assisted immigration alone appears to be a good predictor of observed infestation. It may be that levels of immigration are sufficient at those locations to ensure that establishment is highly successful. In general however, the predicted distribution does not match the observed patterns of infestation throughout the TS/NPA. Importantly, *E. flavipes* is absent at some locations, despite predicted wind-assisted immigration and abundant host plants. These findings suggest that alternate factors influence establishment and population viability beyond numbers of colonists. On-island processes and or propagule pressure provided by other immigration pathways such as the anthropogenic movement of infested sugarcane, may be of equal, or greater relative importance in determining the distribution and abundance of *E. flavipes* in the TS/NPA.

CHAPTER 4 HOST PLANT DISTRIBUTION AND ABUNDANCE

Publication Arising:

Anderson, K. L., Sallam, N. and Congdon, B. C. 2009. The effect of host plant structure on the distribution and abundance of the island sugarcane planthopper, *Eumetopina flavipes* Muir, vector of Ramu stunt disease of sugarcane. *Virus Research* **141,** 247-257 (IF = 2.81, ERA = B).

4.1 INTRODUCTION

Population structuring in insects that have restricted or specific host plants is driven primarily by the quantity, distribution and variability of hosts in both time and space (Denno & McClure 1983; Brower 1985; Lawrence 1994; Worner 2002). Host plant distribution may be relatively continuous, or alternatively, hosts maybe scattered naturally throughout the landscape in small patches that are widely dispersed. Similarly, agricultural management practices may promote fragmentation of host plants. For example, the annual turnover of a crop may result in removal of all infested host plants before replanting begins. Such host plant patchiness and stochasticity generally means that host plant patches may be difficult for insects to locate in either time or space (Thomas 2000; Grilli 2006). When this is true, host plant patches are less likely to be successfully occupied by dispersing insects. If, however, such a host plant patch is occupied successfully, constant immigration and/or positive population growth is required or occupancy is unlikely to continue (MacArthur & Wilson 1967; Hanski 1994; Thomas 2000).

In contrast, insect populations in large, stable host plant patches are more likely to avoid local extinction than those occupying small patches (Williamson 1981; Hanski 1994; Williamson & Fitter 1996; Thomas 2001). Large and stable host patches that cover larger areas should also be easier for dispersing insects to locate (Root 1973). When populations do occur in large, stable host patches, particularly populations that

specialise on that host plant, they tend to exhibit a positive abundance correlation with host availability: this is termed the 'resource concentration hypothesis' (Root 1973). Also, high population abundance generally translates into greater dispersal potential (Denno 1994a; Komonen *et al.* 2004). When many individuals are constantly dispersing between patches i.e. the propagule pressure is high, then connectivity between patches is also high. High patch connectivity may ensure that total population abundance remains relatively stable, that recolonisation of empty host plant patches occurs quickly and that populations remain highly persistent (Hanski 1994; Williamson & Fitter 1996; Hanski & Gilpin 1997; Thomas 2001; With 2002; Allendorf & Lundquist 2003).

E. flavipes appears to be feed specifically on certain species of *Saccharum* L., and has been recorded from *S. spontaneum* L., *S. robustum* E.W. Brandes & Jeswiet ex Grassl, *S. officinarum* L. ('noble' sugarcane) and *S.* 'hybrids' (commercial sugarcane) (Kuniata *et al.* 1994). Throughout PNG, all four of these host types occur and together form a relatively continuous distribution across the landscape. Commercial sugarcane (*S.* hybrids) is grown only in the Ramu Valley, over approximately 7, 500 ha of which approximately 1,000 ha of the total area under sugarcane is managed by small-scale out-growers. *S. spontaneum* and *S. robustum* are considered to be 'wild' and may be the dominant species in suitable habitats throughout PNG (Paijmans 1976). *S. officinarum* is considered a 'native-domesticated' sugarcane and is traditionally cultivated alongside *S. edule* ('pit-pit') and other subsistence food plants such as sweet potato, yam, papaya, cassava and banana (Brandes 1956) (Fig. 4-1). Subsistence agriculture has long been a way of life for Papuans, and today almost every family in PNG still maintains a garden that contains the aforementioned plant species. Garden size can range from a very small plot in a back-yard to a larger plot of 0.4 ha or so. Larger plots may be situated a short walk from the dwelling, and may be tended by several families. *S.* 'hybrids' are grown less commonly in village gardens than *S. officinarum*.

In contrast to PNG, only *S. officinarum* and *S.* hybrids are cultivated in the TS/NPA (Sallam & Anderson 2006). In gardens in both PNG and TS/NPA, the age and number of cultivated sugarcane plants may vary within and between gardens, but in general, subsistence gardening is less prolific in TS/NPA than in PNG. In the TS/NPA, patches of *S. officinarum* and *S.* 'hybrids' are highly fragmented at a regional scale because the plants are scattered over a number of islands and communities. Further

fragmentation also occurs within the islands and communities due to hypothesised variation in the timing of specific cultivation practices.

Figure 4-1. Typical subsistence garden with *S. officinarum*, banana, pineapple, papaya and cassava being grown in a small back-yard plot at Lae, in Papua New Guinea.

The aim of this chapter is to derive a detailed spatial and temporal picture of the effect of differing host plant availability in PNG and TS/NPA on *E. flavipes* distribution and abundance in both regions. This was achieved by first examining *E. flavipes* host usage, host occupancy and abundance in PNG, then by comparing these parameters between PNG and TS/NPA, and finally by determining whether *E. flavipes* population structure varies over time relative to host usage in the TS/NPA. Understanding *E. flavipes* host preferences, as well as how changes in host plant availability influence population structure, is a critical first step in establishing the invasion potential of *E. flavipes* as it colonises new regions; specifically, recolonisation in the TS/NPA.

4.2 METHODS

4.2.1 *Host plant identification*

E. flavipes was collected from throughout central PNG and the TS/NPA (Fig. 4-2). Representative sub-samples of these insects were then sent to Australian Delphacidae expert G. A. Bellis, in Darwin, Australia, to confirm species identification. In order to establish *E. flavipes* host range, known host species (*S. robustum, S. officinarum, S. spontaneum, S.* hybrids), as well as other closely related, potential alternative hosts (from the grass Family Poaceae) were examined in PNG and TS/NPA. The identity and presence of potential alternative hosts in the study area was established from searches of the literature and the Queensland Herbarium HERBRECS database (Grassl 1946; Brandes 1956; Kuniata *et al.* 1994; Kellogg 1998; Hodkinson *et al.* 2002; Queensland Environmental Protection Agency 2005). The identification of all plants from which insects were collected in PNG was undertaken by a single trained Ramu Agri-Industries Ltd. staff member. Host identification in TS/NPA was done by the author (Kylie L. Anderson). If a host plant in the TS/NPA was not clearly identifiable, a specimen was collected and sent to B. M. Waterhouse, Australian Quarantine Inspection Service Botanist, or the Queensland Herbarium, for identification.

4.2.2 *Sampling in Papua New Guinea*

In PNG insects were collected at a total of 11 sites, spread across seven locations. The four main locations visited were Lae (coastal lowlands, two sites), Madang (coastal lowlands, two sites), Goroka (highlands, two sites) and Ramu (commercial sugarcane plantation, two sites) (Fig. 4-2). Three other locations, approximately half-way between Lae and Ramu, Ramu and Madang, and Ramu and Goroka, were also sampled. Sites at each location were approximately 10 – 25 km apart.

At each location/site, insects were collected from as many host types as possible for comparative purposes. When a host was present, at least five stalks from each of five plants per site were sampled. Plant replicates at each site usually occurred in a single garden and were rarely more than 500 m apart; most were much closer. For the five stalks sampled per plant, a visual count of all nymph and adult *E. flavipes* present in the spindle roll was obtained and in the majority of cases, a sub-sample of 5-30 *E. flavipes*

was collected via aspiration. Samples were placed in 100% ethanol and later used to confirm species identification or for further molecular analyses.

Figure 4-2. Map of *E. flavipes* sampling sites at Madang, Goroka, Ramu and Lae in Papua New Guinea, relative to sites in the Torres Strait and northern peninsula area of Queensland, Australia.

4.2.3 ***Sampling in TS and NPA***

Between 13 March and 7 April, 2006, 16 TS and five NPA locations were sampled for *E. flavipes*. Time allowed for sampling at each location varied, and was dependent upon when transport on and off the island was available. At each location, as many sugarcane plants as time permitted (minimum two plants at Injinoo and Moa (Kubin), which were the only ones there) were visited and the presence or absence of *E.*

flavipes recorded for each plant. Up to five stalks from as many plants as the time permitted (minimum two plants at Ugar) were sampled destructively for *E. flavipes* by cutting the spindle roll off the stalk at the first visible leaf joint or 'dewlap' (where the sheath turns into the leaf blade) on each sampled stalk. Leaves from the spindle roll were unfurled one at a time and all *E. flavipes* removed via aspiration, placed in 100% ethanol and transferred to the laboratory for identification and counting.

To determine if the distribution and abundance of sugarcane and *E. flavipes* changed over time, a second survey of the TS/NPA was conducted from 26 March to 17 April, 2008. Seventeen TS and five NPA locations were sampled for *E. flavipes*. *E. flavipes* presence/absence was recorded from every sugarcane plant at each location. Up to five stalks at five plants per location were sampled for *E. flavipes* as described above.

4.3 ANALYSES

4.3.1 *Host plant occupancy*

The effects of host type, region (PNG and TS/NPA), and sample year on patterns of *E. flavipes* host plant occupancy were examined using Pearsons χ^2 tests of proportions. Host plant occupancy was measured as the proportion of the total number of plants sampled at each location that were positive for *E. flavipes* nymphs or adults.

To test for the effect of host type on *E. flavipes* occupancy, samples from all host types from all sampling locations in PNG were compared in a single analysis. This was possible because sampling effort per host type at each location was equivalent. The results of this test indicated that some host types (particularly *S. officinarum* and *S.* 'hybrids') could be pooled for further analyses (see results). Therefore, the level of occupancy in the different regions (PNG and TS/NPA) was examined using presence/absence data from five randomly sampled *S. officinarum* plants from every location in PNG, and TS/NPA where *E. flavipes* occurred in 2008 (Bamaga, Keriri, Yorke, Boigu, Dauan, Saibai, Mabuiag, Badu, Ugar, Waiben, Ngurupai and Erub). Both *S. officinarum* and *S.* 'hybrids' plants were combined in TS/NPA. It was necessary to pool *S. officinarum* and *S.* 'hybrids' plants from TS/NPA as neither host type occurred in sufficient numbers on its own at any location. Changes in occupancy

between sampling years were tested in the TS/NPA only. Presence/absence data from every plant visited at all TS/NPA locations positive for *E. flavipes* in either year of sampling were used. The test was repeated for 'stable' TS/NPA locations positive for *E. flavipes* in both years of sampling (see results).

4.3.2 *E. flavipes abundance on occupied plants*

Using plants known to be occupied, the relationships between host plant type, and/or regional locations and sample year on *E. flavipes* abundance were quantified. Abundance relationships for nymphs and adults were analysed separately as the number of nymphs on a plant is a measure of *E. flavipes* breeding success, whilst the number of adults is an indication of *E. flavipes* breeding activity and dispersal potential. Of the four host types, only *S. officinarum* and *S. edule* had at least three, with a maximum of six, occupied plants per site. Therefore, a Paired t-test was used to examine the effect of these two host types on *E. flavipes* abundance, independent of any site effects. Data from this analysis were bordering on non-normal, therefore a Wilcoxon Signed Ranks test with marginal homogeneity test was used to confirm results from the Paired t-test.

Welch ANOVA was used to examine the effect of host structure on *E. flavipes* abundance between regional locations (PNG and TS/NPA). The Welch statistic is preferable to the *F*-statistic when the assumption of equal variances may be invalid (SPSS Inc. 2004). Data from at least five or six occupied *S. officinarum* plants at each PNG location and from one to five at each TS/NPA location were used. Sampling locations in PNG and TS/NPA were spread over a similar spatial scale and sampling effort was equivalent. Sample sizes were unavoidably smaller per location in the TS/NPA because of clear differences in occupancy rates (see results). A Mann-Whitney test was used to examine the effect of sample year on *E. flavipes* abundance throughout the TS/NPA. Plants from all TS/NPA locations that were positive for *E. flavipes* in either year of sampling were used. The test was repeated for 'stable' TS/NPA locations positive for *E. flavipes* in both years of sampling (see results).

4.3.3 *Host plant occupancy and abundance in TS/NPA over time*

Regression analysis was used to examine the relationship between host plant occupancy and *E. flavipes* abundance over time in the TS/NPA. Plants sampled from TS/NPA locations that were positive during either sampling year were used in the regression analysis. Then, hierarchical cluster analysis using average linkage between groups, and based on squared Euclidian distance of standardised variables, was used to group TS/NPA locations that were homogenous with respect to level of host plant occupancy and *E. flavipes* abundance.

For all analyses, data normality and equality of variance assumptions were met, or corrections applied, when parametric tests were used. All statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc. 2004).

4.3.4 *Cultivation practices in the TS/NPA*

Cultivation practices can have a major impact on host plant patch structure and stability, and therefore affect the distribution, abundance and persistence of *E. flavipes* populations. To assist with the interpretation of results, gardeners throughout the region were interviewed during the 2008 survey in an attempt to identify trends in plant origin and cultivation practices. Questions asked were (1) Did the sugarcane in your garden come from this island, another island or PNG? If another island, which one? (2) Do you practise any pest control on the sugarcane? If yes, what type? (3) Do you harvest and replant your sugarcane? If yes, what time of the year and why? (4) Does everyone on the island harvest and replant at the same time? (5) How do you replant your sugarcane? (6) Once planted, how do you look after your sugarcane?

4.4 RESULTS

4.4.1 *PNG: Host range, host plant occupancy and abundance*

In PNG, a total of 224 plants were sampled over seven locations. Potential host types sampled ('?' denotes uncertain identifications) were *S. edule*, *S. officinarum*, *S.*

robustum, *S. robustum* 'mountain form', *S. spontaneum*, *S.* 'hybrids', *Pennisetum purpureum*, ?*P. purpureum*, ?*Sorghum* sp. and *Miscanthus* sp.. *P. purpureum*, ?*P. purpureum*, ?*Sorghum* sp. and *Miscanthus* sp were each sampled at one site. *S. edule*, *S. officinarum* and *S. robustum* (it is likely that *S. robustum* 'mountain' form is a variety of *S. robustum*, therefore the two host types were pooled in further analyses) occurred at every sampled site. In contrast, *S.* 'hybrids' sugarcane occurred only at Ramu, and *S. spontaneum* was present at four of the seven sampled locations. The identification and number of host species sampled per location is summarised in Table 4-1.

Table 4-1. Number and identity of potential *E. flavipes* host species sampled per location and site in Papua New Guinea, with occupancy rate per host type.

Location	Host / Site	E	O	R	S	H	P	?P	So	M
Lae	1	6	6	5	5					
	2	5	5	5			4	1	5	
Ramu	1	5	5	5	5	5				
	2	5	5	5	5	10				
Madang	1	5	6	5						
	2	5	5	5						
Goroka	1	5	5	6	5					
	2	5	5	6						
Between Lae and Ramu	1	5	5	5	5					
Between Ramu and Madang	1	5	5	5						
Between Ramu and Goroka	1	5	5	5						5
Total plants sampled		56	57	56	25	15	4	1	5	5
Number plants occupied		37	57	28	4	15	0	0	0	0
Proportion plants occupied within host type		66	100	50	16	100	0	0	0	0

Host plant codes: *Saccharum edule* (E), *S. officinarum* (O), *S. robustum* (R), *S. spontaneum* (S), *S.* 'hybrids' (H), *Pennisetum purpureum* (P), ?*Pennisetum purpureum* (?P), ?*Sorghum* sp. (So) and *Miscanthus* sp. (M).

Up to four different *Eumetopina* species were collected from the host types sampled; identification of species other than *E. flavipes* will be reported elsewhere. *E. flavipes* was detected on five host types *S. edule*, *S. officinarum*, *S. robustum*, *S. spontaneum* and *S.* 'hybrids'. There was a significant difference in *E. flavipes* occupancy rate between host types in PNG (Pearson $\chi^2 = 72.72$, d.f. = 4, $P < 0.001$). All sampled *S. officinarum* and *S.* 'hybrids', 66% of *S. edule*, 50% of *S. robustum* and 16% of *S. spontaneum* plants were infested (Table 4-1).

S. edule plants were consistently occupied by *E. flavipes* at Lae, Madang and Goroka site-1, but *S. edule* at Goroka site-2 was not occupied. There was consistently less than 50% occupancy of *S. robustum* plants by *E. flavipes* at Lae, Madang and Goroka. At Lae, Madang and Goroka, variable numbers of *S. edule* and *S. robustum* plants were occupied, whereas at Ramu all were occupied. *S. spontaneum* plants were occupied at the lowest rate of all host types. A total of 11 *E. flavipes* nymphs were detected on four of 25 plants sampled (nine nymphs on two plants at Lae, one nymph on one plant at Ramu and one nymph on one plant at Goroka), whereas no adults were detected. The identity of these specific nymphs has not yet been confirmed, and nymphs and adults of undescribed *Eumetopina spp*. were often sampled on *S. spontaneum*. Therefore, if at all, *S. spontaneum* appears to be a very poor host for *E. flavipes* and was not included in further analyses. The highest recorded abundances of *E. flavipes* nymphs and adults on individual plants per host types are summarised in Table 4-2.

Table 4-2. Highest recorded abundance of *E. flavipes* nymphs and adults on different host plant types in Papua New Guinea.

Life stage	Host type	Location	Abundance
Nymphs	*S. edule*	Lae	65
	S. officinarum	Madang	287
	S. robustum	Ramu	201
	S. 'hybrids'	Ramu	17
Adults	*S. edule*	Lae	40
	S. officinarum	Lae	49
	S. robustum	Ramu	15
	S. 'hybrids'	Ramu	3

Due to the high variability and consistently low occupancy rates observed on *S. robustum* at Lae, Madang and Goroka this host type was not included in the abundance analyses across these sites. Therefore, *E. flavipes* abundance was only compared between *S. edule* and *S. officinarum* at the Lae, Madang, Goroka and Ramu sites. There was no significant difference in nymph or adult abundance between *S. edule* and *S. officinarum* at Lae, Madang, Goroka, Ramu and between Ramu and Madang, nor adult abundance per plant between *S. edule* and *S. officinarum* at Lae, Madang or Ramu (Paired t-test; nymphs t = -0.958, d.f. = 7, $P > 0.05$; adults t = -0.794, d.f. = 5, $P > 0.05$; Wilcoxon signed ranks test; nymphs Std. MH statistic = -0.963, $P > 0.05$; adults Std. MH statistic = -0.825, $P > 0.05$). The pooled location mean abundance (1 SE) of *E. flavipes* nymphs on *S. edule* and *S. officinarum*, respectively, was 12 (5) and 20 (9), and for adults was 5 (2) and 8 (3) respectively. Populations of *E. flavipes* were always more variable on *S. officinarum* than *S. edule*, but were never consistently higher on either *S. officinarum* or *S. edule* at any location.

Ramu was the only location where a comparison was possible between the abundance of *E. flavipes* nymphs and adults on each of the four main host types *S. edule*, *S. officinarum*, *S. robustum* and S. 'hybrids'. The abundance of nymphs at Ramu was significantly different between *S. edule*, *S. officinarum*, *S. robustum* and *S.* 'hybrids' (Welch ANOVA, $F_{3,\ 18.94} = 3.581$, $P < 0.05$). Despite the significance of the Welch ANOVA, the Games-Howell post-hoc test did not identify specific host types that were significantly different. Therefore, the significant difference in nymph abundance between host types detected by ANOVA is marginal and must be interpreted cautiously. Nymphs appear more abundant and more variable on *S. robustum* than on the other host types (Fig. 4-3).

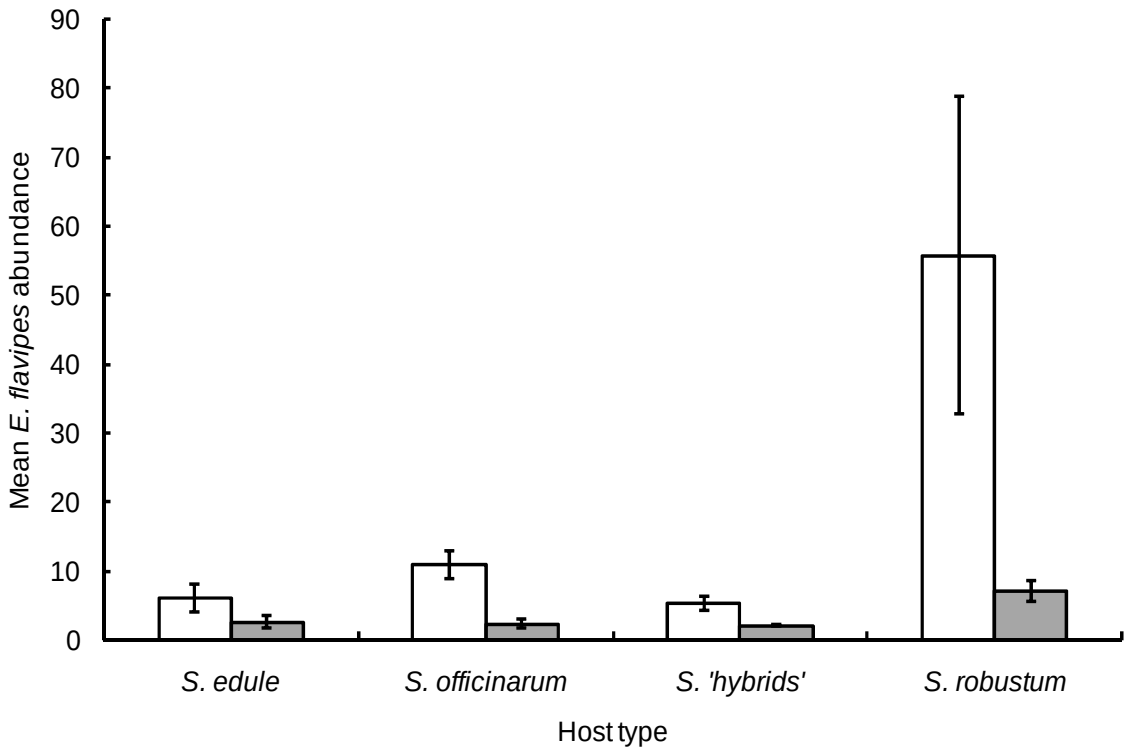


Figure 4-3. Mean *E. flavipes* nymph (□) and adult (■) abundance on four different host types at Ramu, PNG (2 SE).

However, one particular *S. robustum* plant at Ramu, which was a clear outlier, supported an average of 201 nymphs, which means that it was much more heavily infested than any other *S. robustum* plants sampled at Ramu, or other sites, where the mean abundance was less than an average of four per plant. When the Welch ANOVA was re-run with this individual plant removed, there was no significant relationship between nymph abundance and host type (Welch ANOVA, $F_{3, 17.83} = 3.18$, $P = 0.05$).

The mean abundance of adults per plant was significantly different between *S. edule, S. officinarum, S. robustum* and *S.* 'hybrids' at Ramu (Welch ANOVA, $F_{3, 18.66} = 5.570$, $P < 0.05$). Games-Howell post-hoc tests revealed significantly more adults on *S. robustum* than *S. edule, S. officinarum* or *S.* 'hybrids' (Fig. 4-3).

The mean abundance of *E. flavipes* adults (SE) on *S. robustum* plants was 7 (2). In comparison, the mean abundance of adults on occupied *S. robustum* plants at Lae, Madang and Goroka was less than two, again much less than their mean abundance at Ramu. Therefore, heavy infestation of *S. robustum* by nymphs and adults at Ramu appears an exception rather than a trend. *E. flavipes* is usually not as abundant on *S. robustum* as it is on other host types.

4.4.2 *PNG and TS/NPA: host plant occupancy and abundance*

There was a significant difference in host plant occupancy rate between PNG and TS/NPA (Pearson χ^2 = 40.07, d.f. = 1, $P < 0.001$). All *S. officinarum* host plants sampled in PNG (n = 57) were occupied, compared to 44% of the total number of *S. officinarum* and *S.* 'hybrids' plants sampled in TS/NPA (n = 60). However, when nymph and adult *E. flavipes* occurred on a plant, the overall abundance per infested plant was not significantly different between PNG and TS/NPA (ANOVA nymphs, $F_{1, 79} = 0.791$, $P > 0.05$; adults, $F_{1, 75} = 0.331$, $P > 0.05$) (Fig. 4-4). The heaviest individual infestation of nymphs in PNG was at Madang (an average of 287 nymphs on the plant), and in the TS/NPA was at Ngurupai (an average of 80 nymphs on the plant). For adults, the heaviest individual infestation in PNG occurred at Lae (an average of 49.2 adults on the plant), and in the TS/NPA at Bamaga (an average of 18 adults on the plant).

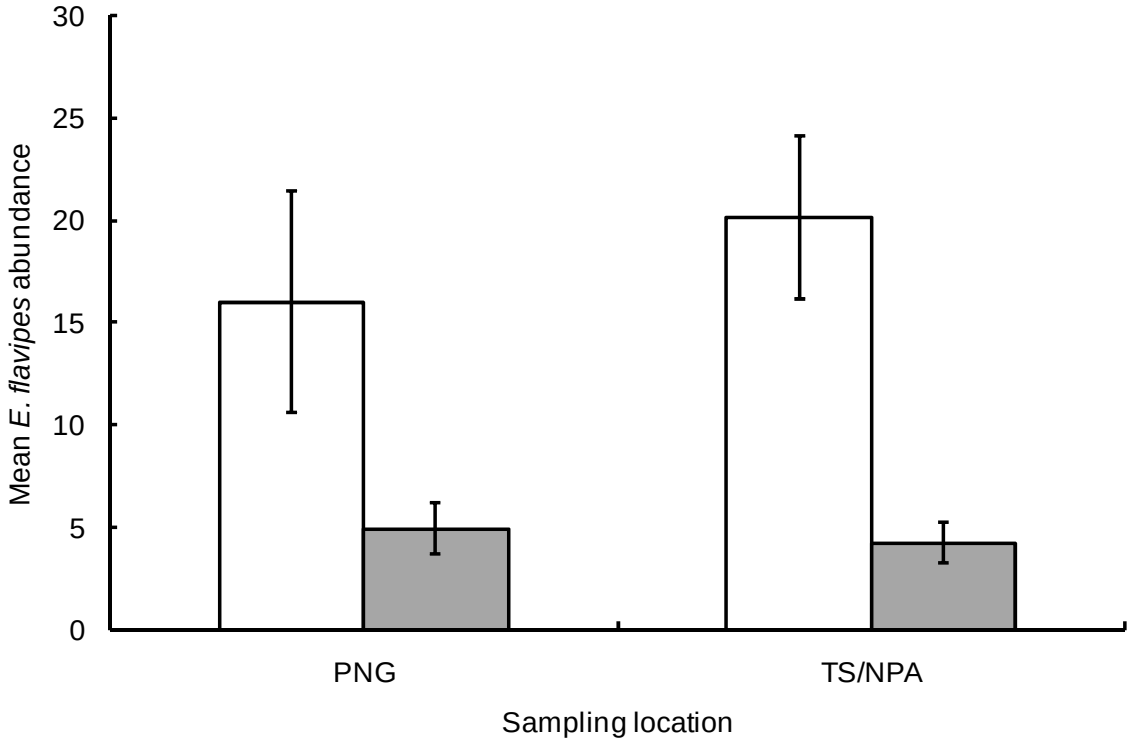


Figure 4-4. Mean abundance of *E. flavipes* nymphs (□) and adults (■) per plant (2 SE) in PNG and TS/NPA.

4.4.3 *TS/NPA: Host plant distribution, occupancy and abundance over time*

In 2006, 21 locations were visited and a total of 230 *S. officinarum* and *S.* 'hybrids' plants were sampled. In 2008, 22 locations were visited and a total of 545 *S. officinarum* and *S.* hybrids plants were sampled. *E. flavipes* distribution was highly variable at many locations in the Torres Strait over time (Fig. 4-5). However, at ten locations, Boigu, Dauan, Saibai, Erub, Masig, Mabuiag, Badu, Waiben, Ngurupai and Bamaga, *E. flavipes* was detected in each year (Fig. 4-5). These locations were termed 'stable' because of the continued presence of *E. flavipes* compared to other locations. Sugarcane (*S. officinarum* or *S.* 'hybrids') was not present at Seisia in 2006, in Umagico in 2006 and 2008, and at Kubin in 2008, but occurred at every other location sampled. Potential alternative hosts sampled, and on which there were no *E. flavipes*, were ?*P. purpureum* (Bamaga and Horn), *?Phragmites australis* (Badu), *Zea mays* (Ugar and Mer), *?Rottboellia cochinchinensis* (Keriri and Mer), *Sarga plumosum* (near Seisia) and *Cymbopogon citratus* (Iama). A large, wild patch of ?*S. robustum* was discovered on Mer in 2008, and a herbarium specimen submitted to Queensland Herbarium (submission number KLA1001). *E. flavipes* was not detected on the ?*S. robustum*, but only a few peripheral plants were sampled as the patch was very tall and dense and surrounded by thick forest.

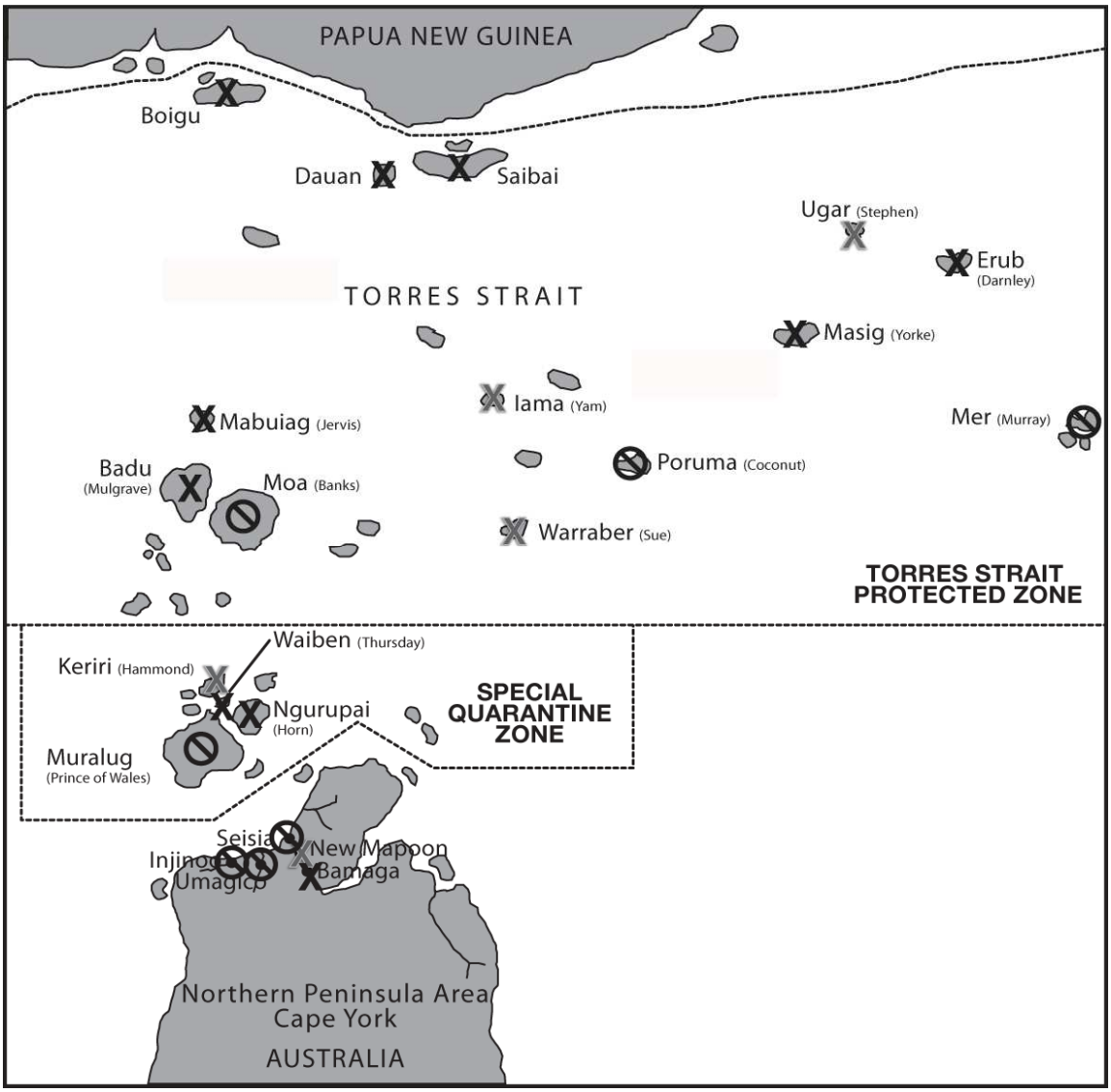


Figure 4-5. Map of the Torres Strait and northern peninsula area of Queensland, Australia, sampling sites with results from 2006 and 2008 field surveys. **X** = *E. flavipes* detected in both years of sampling, X = *E. flavipes* detected in either 2006 or 2008, ⊘ = *E. flavipes* not detected in either year of sampling.

Overall occupancy of host plants in the TS/NPA did not change significantly between years (Pearson χ^2 = 2.69, d.f. = 1, $P > 0.05$) (Table 4-3). Similarly, there was no significant difference in overall occupancy of host plants at the stable locations between years (Pearson χ^2 = 2.3, d.f. = 1, $P > 0.05$) (Table 4-3).

Overall *E. flavipes* abundance in the TS/NPA did not differ significantly between sampling years (Mann-Whitney z = -1.34, $P > 0.05$) (Table 4-3). Also, abundance did not differ between years at stable locations (Mann-Whitney z = -0.99, $P > 0.05$) (Table 4-3).

Table 4-3. Comparison between *E. flavipes* host plant occupancy and abundance between sampling years throughout TS/NPA and at stable locations.

Year	Occupancy Rate (%)		Mean Rank Abundance	
	Entire TS/NPA	Stable locations	Entire TS/NPA	Stable locations
2006	44 (n=179)	49 (n=141)	39 (n=43)	32 (n=33)
2008	37 (n=419)	42 (n=364)	33 (n=29)	28 (n=26)

There was a significant positive relationship between the level of host plant occupancy and ln (x + 1) transformed mean *E. flavipes* abundance. The relationship may be described by both logarithmic and linear models (ANOVA, logarithmic $F_{1, 22} = 13.605$, $P < 0.01$, Adj $R^2 = 0.35$; linear $F_{1, 22} = 8.18$, $P < 0.01$, Adj $R^2 = 0.24$), and although the non-linear model provides a better fit to the data, the variation explained by either model was relatively low (Fig. 4-6).

These relationships suggest that although the rate of host plant occupancy is highly variable throughout the TS/NPA, an increase in host plant occupancy results in increased *E. flavipes* abundance. However, regardless of the rate of host plant occupancy, average *E. flavipes* numbers per plant appear to trend towards an upper limit of approximately 60.

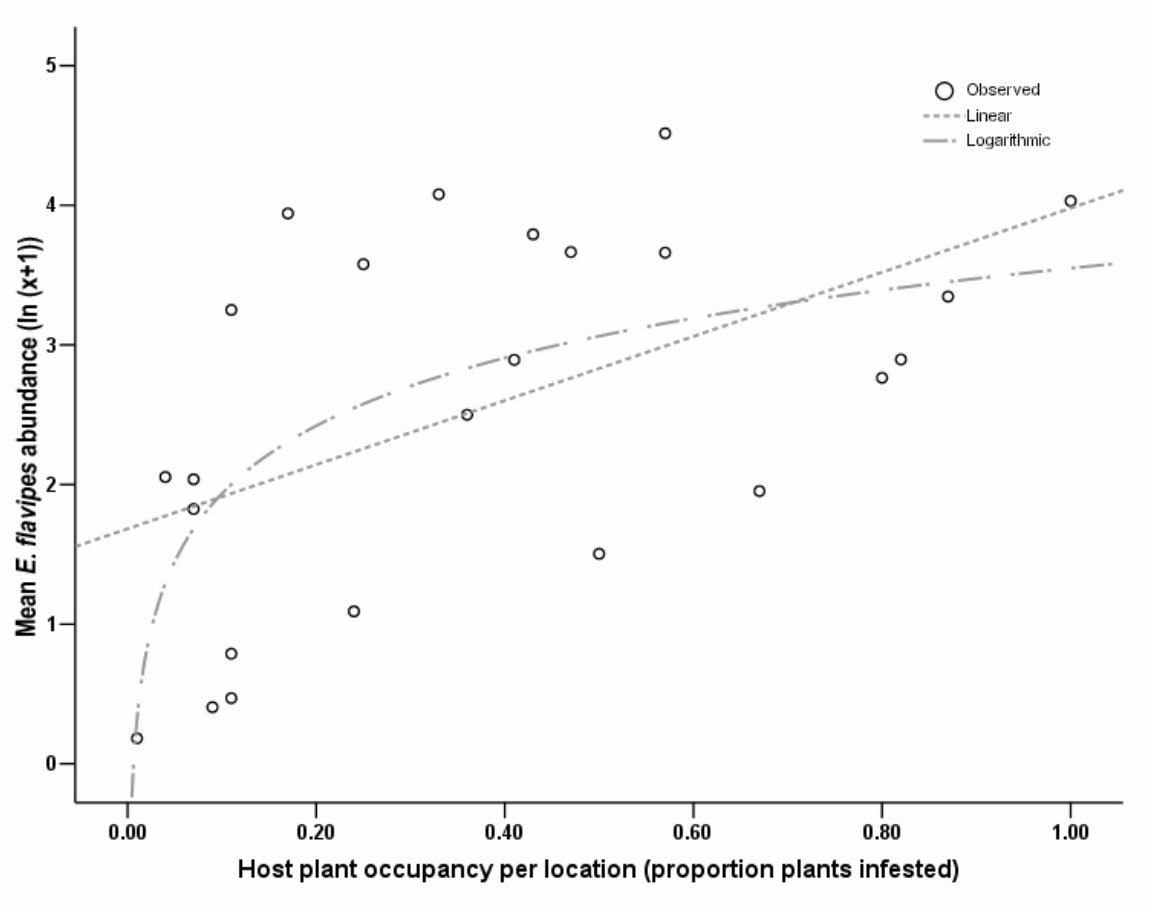


Figure 4-6. Relationship between the proportion of plants infested and the mean abundance of *E. flavipes* per plant (ln (x + 1) transformed) in the Torres Strait and northern peninsula area of Queensland.

After hierarchical cluster analysis, five TS/NPA location clusters were evident at a rescaled distance of 5.5 (Fig. 4-7). However, these may be grouped into two major clusters. Cluster 1 contains stable locations where *E. flavipes* infestation was consistent but decreasing or low over time (low proportion of plants infested with a low abundance of *E. flavipes*), or locations where *E. flavipes* was detected in only one or other year of sampling (Fig. 4-7).

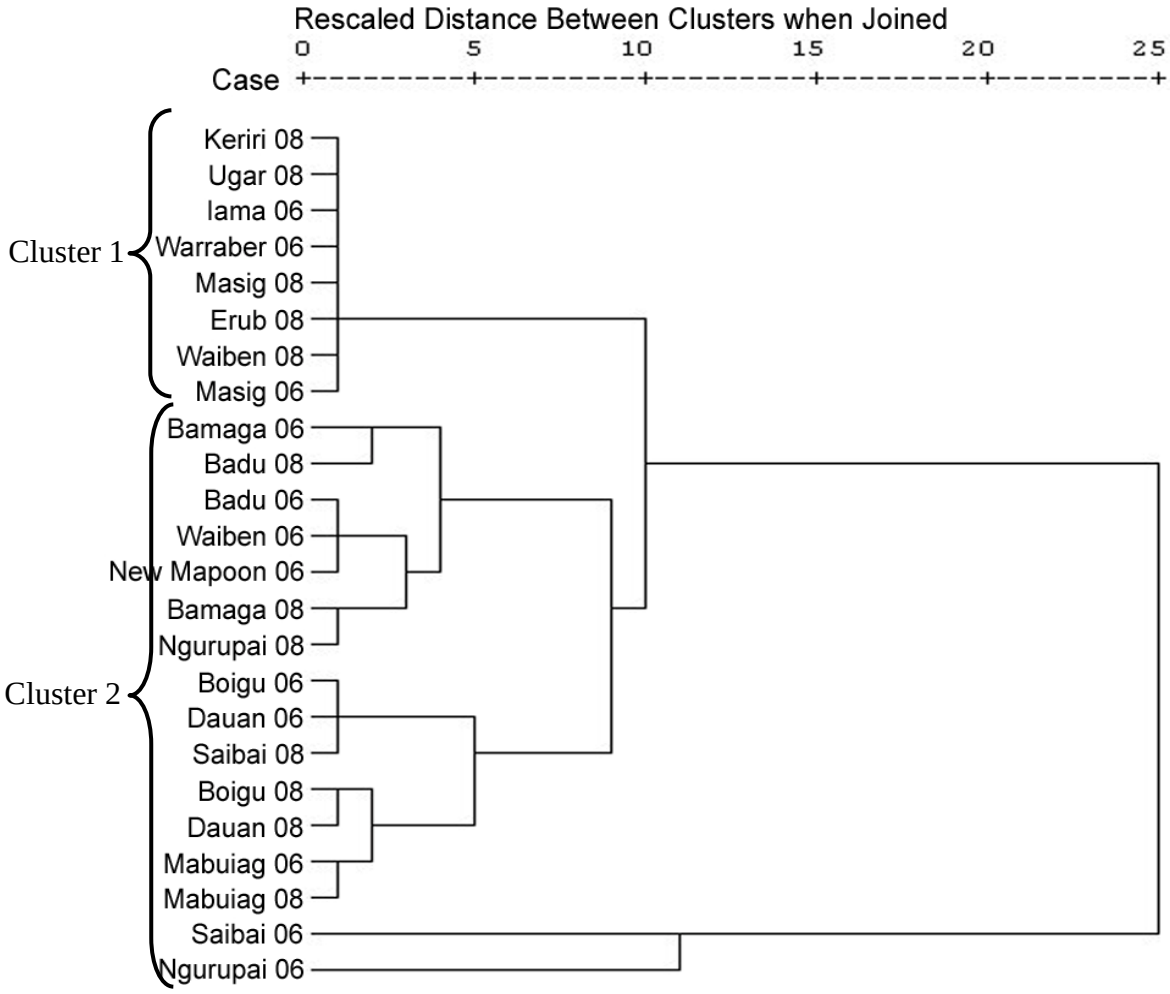


Figure 4-7. A dendrogram displaying results from a cluster analysis of Torres Strait and northern peninsula area of Queensland locations over two years of sampling host plant occupancy and mean *E. flavipes* abundance per plant. Two major clusters are shown.

When *E. flavipes* was detected at a specific location in the first year of sampling but not the second, it was because the occupied plants no longer occurred, and when *E. flavipes* was detected in the second year only, it was usually on new plantings. Therefore, cultivation practices directly affect the presence or absence of *E. flavipes* in the TS/NPA. With the exception of Keriri 08 and Waiben 08, all locations in the first cluster occur in the Central and Eastern group of TS islands (Fig. 4-8).

Cluster 2 includes seven of the ten locations at which *E. flavipes* was detected in both years of sampling; Bamaga, Boigu, Dauan, Saibai, Badu, Mabuiag and Ngurupai (Fig. 4-7). At each of these locations, the same large, well-tended individual host plants or host plant patches occurred and sustained consistent, medium to heavy infestations in

each year of sampling. Every location in Cluster 2 cluster occurs in the Top Western, Western, Inner or NPA group, and these locations run in an almost straight line north-south along the western border of the TS archipelago (Fig. 4-8).

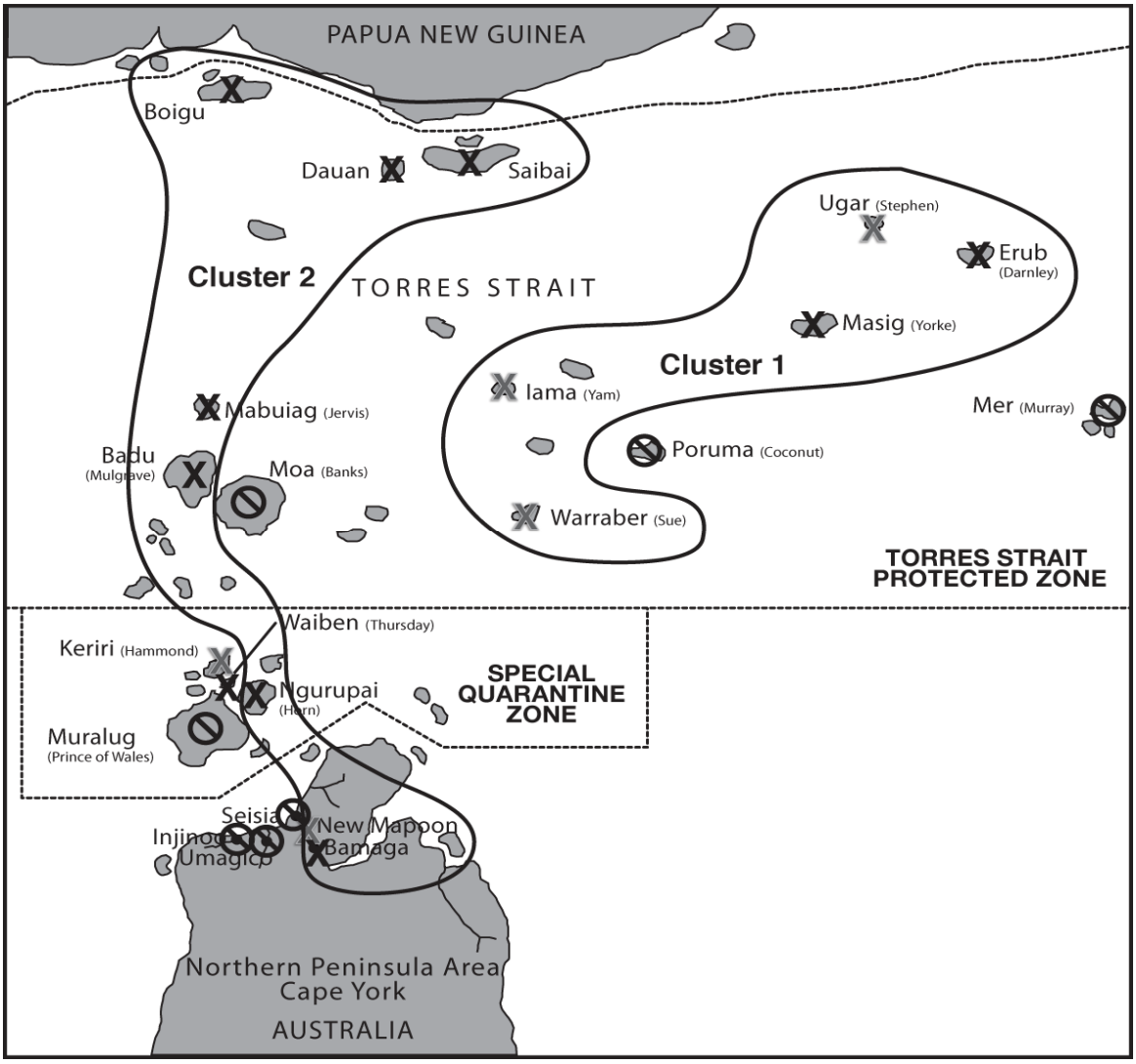


Figure 4-8. Map of the Torres Strait and northern peninsula area of Queensland displaying two main clusters based upon *E. flavipes* host plant occupancy and mean *E. flavipes* abundance per plant. **X** = *E. flavipes* detected in both years of sampling, X *E. flavipes* detected in either 2006 or 2008, ⊘ = *E. flavipes* not detected in either year of sampling.

4.4.4 *Garden cultivation practices in the TS/NPA*

A total of 24 people from Saibai, Boigu, Moa (Kubin), Moa (St Pauls), Badu, Waiben, Mer, Mabuiag, Warraber, Poruma, Iama, Ugar, Erub, Keriri, Ngurupai and New Mapoon were interviewed. Sharing of vegetative planting material between gardeners appears very common throughout the TS/NPA. Planting material on the NPA appeared to be sourced from both within and between other NPA communities, whereas planting material at TS locations appeared to be sourced mainly on-island. There was a general feeling that illegal planting material may still be imported into the TS/NPA from PNG, and moved throughout the TS/NPA, despite Quarantine regulations which prohibit such movement (Australian Government 1908). It appeared to be standard practice throughout the TS/NPA that at least once per year at around the same time, sugarcane was harvested and replanted. Replanting occurs using stem cuttings either with the 'tops' (apical tip complete with leaves), and/or the 'bone' (stalk without leaves), which are cut from existing plants. However, harvesting and replanting may take place at any time of the year. The level of post-planting care appears to vary considerably and often determines the level of successful plant establishment. If cut sections are not replanted, they are given to other families at the same location, or at other locations (although this may happen at any time during the year), or left in the sun to dry and then burned.

4.5 DISCUSSION

In PNG, *E. flavipes* is monophagous (i.e. feeds on plant species from a single genus) on *S. officinarum*, *S. robustum*, *S. edule* and *S.* 'hybrids'. Apart from *S.* 'hybrids' which were available only at Ramu, all host plants of *E. flavipes* are widely available throughout PNG. The fact that *E. flavipes* can occupy four very closely related host types is not surprising, given that most Delphacidae are associated with particular monocotyledonous plant taxa (Wilson *et al.* 1994). It is generally accepted that the genus *Saccharum* evolved and diversified in PNG, which is why PNG is very rich in *Saccharum* spp. (Brandes 1956; Clayton & Renvoize 1999). Phylogenetically, *S. edule*, *S. officinarum* and *S. robustum* are more closely related to each other than they are to *S. spontaneum* (Irvine 1999; Amalraj & Balasundaram 2006), whilst modern

commercial *S.* 'hybrid' sugarcanes are a cross between *S. officinarum* and *S. spontaneum* (Irvine 1999). Therefore, the four major host types of *E. flavipes* are very closely related. That, along with the fact that PNG is as rich in *Eumetopina spp*. as it is in *Saccharum spp*. and cultivars, provides support for the theory that *E. flavipes* and *Saccharum* may have co-evolved (M. R. Wilson, National Museum Wales, *pers. comm*.).

Results of this study suggest that *S. spontaneum* is not a favourable host for *E. flavipes*. This result is unexpected given the close relationship between *S. spontaneum* and the other host types, and that a previous study has recorded *E. flavipes* as abundant on *S. spontaneum* in PNG (Kuniata *et al.* 1994). The reason for this discrepancy is currently unknown, but it may be due to either i) temporal or spatial variation in *E. flavipes* occupancy of *S. spontaneum* due to unknown ecological factors, or ii) the presence of as yet undescribed cryptic *Eumetopina spp*. on *S. spontaneum*. Further study, particularly on the taxonomy of the *Eumetopina* complex, is required to clarify this issue.

In PNG, occupancy rates differed significantly between the four host types. These differences could be due to either behavioural preference (i.e. insect choice), or differential survival on different host types. This study did not test possible functional reasons for the variation, but it is well known that successful host plant colonisation is greatly influenced by the behavioural and physiological adaptations of the herbivore (Wasserman & Futuyma 1981). Therefore, it is reasonable to assume that because the *S. officinarum* and *S.* hybrids plants sampled were always occupied (i.e. colonised), that *E. flavipes* may be most suited to *S. officinarum* and S. 'hybrids' for a variety of behavioural and/or physiological reasons. However, *E. flavipes* is also clearly able to occupy and use *S. edule* and *S. robustum*, although to a lesser degree.

In PNG, the mean abundance of *E. flavipes* did not differ between *S. edule* and *S. officinarum* and throughout most of PNG, *E. flavipes* was much less abundant on *S. robustum* than on other host types. This general pattern of relative distribution was reversed at Ramu, where *E. flavipes* abundance was higher on *S. robustum* than on the other three host types. Importantly, this site-specific result was driven by high abundance on one particular *S. robustum* plant that was located next to a large, recently deforested patch of rainforest which in turn, was located beside a local garden that was not sampled. Taken together, these findings suggest that *S. robustum* may be a sub-

optimal host compared to the other three host types, but that effective use of this sub-optimal host may occur under specific ecological circumstances.

While *E. flavipes* is clearly able to achieve high abundances on all four principal host types, there was also considerable variation in insect numbers from plant to plant both within and between hosts. Therefore, it appears that once occupied, particular plants regardless of host type may have specific attributes which favour increased abundance of *E. flavipes*. Specifically for herbivorous insects such as *E. flavipes*, various attributes including the presence of non-host plants in or near the host plant patch, the distance between host plants, the geographical size of the patch and/or of individual plants, or differences in plant structural physiology or nutritional quality etc. can cause variations in abundance (Denno 1994a). It is not known specifically which, if any, of these mechanisms drive differences in *E. flavipes* abundance, but findings suggest they may be at least, if not more important than host-specific differences between the principal hosts tested.

Of the four *Saccharum* host types used regularly by *E. flavipes* in PNG, only the two apparently most favourable, *S. officinarum* and *S.* 'hybrids', occurred throughout the TS/NPA. Occupancy rates for these hosts differed markedly between PNG and TS/NPA, in that all of the *S. officinarum* plants sampled in PNG were occupied, whereas fewer than half of the total number of *S. officinarum* and *S.* 'hybrids' plants sampled in the TS/NPA were occupied. In PNG, *S. officinarum* and *S. edule* occurred at every location, and *S. edule* was planted adjacent to, or in the same garden as *S. officinarum*. Large patches of wild *S. robustum* also occurred at most locations. As predicted under the resource concentration hypothesis and other resource availability theory (Andrewartha & Birch 1954; Root 1973; Schowalter 2000), the presence of abundant, stable and multiple host types implies that both resources and therefore colonising individuals should be readily and consistently available both within and between locations in PNG. The consistently greater level of occupancy observed in PNG supports this hypothesis.

In the TS/NPA, host plant occupancy was less than 50 %. The structure of host plants in the TS/NPA differed vastly from that in PNG, in that host plants were not equally abundant at different locations, were sometimes totally absent, and were highly fragmented due to ocean barriers between the majority of locations. Theoretically, the occurrence of insects is dependent upon how capable individuals are at 'tracking' changes in host distribution and abundance, and if host plant structure is stochastic in

space and time, tracking may be very difficult (Thomas 1994). Findings suggest that there are several specific locations scattered throughout the TS/NPA where cultivation practices result in frequent and sudden loss of occupied host patches. The loss of host appears to be directly responsible for either a reduction in the overall rate of occupancy, or local extinction over both the short or longer term. At these locations, new colonisations and subsequent population establishment can only occur if host plant patches are replanted and colonists are available and able to track and reach them from outlying locations.

Although the occupancy rate of host plants in TS/NPA was much lower than in PNG, the mean abundance of *E. flavipes* per occupied plant did not differ between the two regions. There was evidence that this was due to an abundance threshold exhibited by *E. flavipes* populations on individual plants. These findings conflict with expectations under the resource concentration hypothesis that *E. flavipes* should be more abundant per individual plant in PNG because the number and availability of host types is greater there. In many insects, crowding on host plants triggers dispersal (Schowalter 2000). If this is true of *E. flavipes* it would explain my results and suggest that as populations on individual plants approach the abundance threshold, individuals are dispersing from the plant and may be colonising unoccupied host plants nearby. If colonisation was successful, abundance on these plants would also increase to a threshold, and the process thus repeat until all plants at a location are occupied at similar abundance. *E. flavipes* breeding potential appears to be similar on occupied plants throughout PNG and TS/NPA, therefore the differences in the results obtained for each region may relate to all *S. officinarum* plants in PNG being occupied at, or near this threshold abundance whilst those in the TS/NPA are not. If true, an important implication of this finding is that it may be possible to estimate absolute *E. flavipes* population growth potential at any specific location based upon the number of plants present and/or occupied. Locations which contain high population growth potential are likely to produce large numbers of dispersing colonists due to the high propagule pressure, therefore control of *E. flavipes* could be targeted preferentially at such locations.

While both the distribution and persistence of *E. flavipes* populations in the TS/NPA was highly variable, a number of clear, general patterns of infestation were observed. First, *E. flavipes* was not detected at several locations despite the presence of host plants. Second, a group of Central and Eastern Islands tended to sustain either

consistent low infestations or populations that were prone to local extinction. Third, stable, medium to heavy infestations were supported on islands that formed a relatively unbroken chain along the western edge of the TS, theoretically connecting PNG to mainland Australia at the NPA. Although it is now clear that cultivation practices impact heavily upon host plant occupancy and population persistence at many locations (particularly those where infestations rates are low), survey data suggest that cultivation practices are similar throughout the TS/NPA. This means that in general, site-specific differences in cultivation are unlikely to be the principal factor responsible for the lack of insects at some locations and increased persistence of populations at others.

One reason for increased persistence of *E. flavipes* populations at only a subset of locations may be because there are more gardens at these locations, and therefore a larger pool of hosts. More gardens means that a greater proportion of hosts would remain available at any one point in time despite most of the sugarcane in gardens being replanted at some time during each year. However, whilst the presence of refuge populations associated with greater host abundance may explain increased persistence at stable locations, it does not account for re-establishment at locations where *E. flavipes* populations have become locally extinct. Therefore, recolonisation from off-island sources must also be occurring in the TS/NPA. So, it is possible that locations with greater *E. flavipes* persistence over time may also have greater rates of immigration from off-islands, whilst islands that are recolonised only after long periods of *E. flavipes* absence may have much lower rates of immigration.

Results of this chapter clearly show that changes in host plant distribution, abundance and availability are important in regulating *E. flavipes* population structure at a local scale. Cultivation practices, which vary throughout the Torres Strait, appear to be primarily responsible for local extinction, and/or the maintenance of very low infestations in some areas of the Torres Strait.

CHAPTER 5 POPULATION CONNECTIVITY IN THE TS/NPA

Publication Arising:

Anderson, K. L. and Congdon, B. C. In review. Reconciling invasion route and dispersal mechanisms with population genetic characteristics of a quarantine pest. *Molecular Ecology* (IF = 6.457).

5.1 INTRODUCTION

The environmental and economic costs of biological invasions are key issues for many countries (Pimentel *et al.* 1999). Understanding the ecological factors contributing to invasion success is important when seeking to implement effective control strategies for invasive species. Foremost among factors shown to influence invasion success is the ability of an organism to disperse to new regions (Lockwood *et al.* 2007). If an invasive species is regularly transported along multiple pathways, then the probability of its successful establishment is increased (Kolar & Lodge 2001). Importantly, the dispersal history of an organism may be reflected in the current spatial pattern of population genetic structure (Sakai *et al.* 2001; Excoffier *et al.* 2009). Specifically, population genetic data can provide valuable insight into an organisms dispersal pathways (Congdon *et al.* 1997; Alvarez *et al.* 2007; Suhr *et al.* 2010), invasion routes (Zepeda-Paulo *et al.* 2010) and more broadly, overall invasion potential and pest status (Darling *et al.* 2008; Gardner-Santana *et al.* 2009; Jiang *et al.* 2010). Therefore, when coupled with additional ecological information on life history strategy, population genetics analyses provides a strong basis on which to formulate pest management strategies (Rollins *et al.* 2009).

On infested sugarcane, *E. flavipes* resides among the growing leaf-rolls. *E. flavipes* is widespread throughout PNG (Magarey *et al.* 2002), where it is considered native (Wilson, M. R. 2006, pers. comm.). Results from Chapter four reveal that in PNG, *E. flavipes* commonly occurs on four species of *Saccharum; S.* 'hybrids' grown in

commercial plantations in the Ramu Valley, *S. officinarum* and *S. edule* which are grown in residential gardens, and *S. robustum* which grows wild and is highly abundant in suitable habitat throughout PNG (Paijmans 1976). These four host species form a relatively continuous distribution across the landscape, likely promoting large and stable *E. flavipes* populations in PNG (Chapter four; Anderson *et al.* 2009).

A different situation exists in the TS/NPA, where *E. flavipes* occurs on the only two host species present, *S.* 'hybrids' and *S. officinarum*. These hosts are cultivated for local use only, but also occur as untended plants growing wild at some locations (Chapter four; Anderson *et al.* 2009). Both long term survey data (Gough & Petersen 1984; Chandler & Croft 1986; Allsopp 1991; Grimshaw 1997; Magarey 1997; Magarey 2003; Anderson 2005) and recent intensive sampling confirm that *E. flavipes* presence is highly variable in space and time, and local extinctions and recolonisation occur frequently (Chapter four; Anderson *et al.* 2009).

Simulation modelling suggests that southward wind-assisted immigration is likely to occur from PNG into the TS/NPA during the summer monsoon season (Chapter three; Anderson *et al.* 2010). The resulting number of immigrants per island is a function of wind direction and distance from PNG (Chapter three; Anderson *et al.* 2010). As discussed, wind is known to facilitate long-distance dispersal in planthoppers (Kisimoto & Rosenberg 1994) and a pattern of declining dispersal probability with distance from a source as suggested for *E. flavipes* in Chapter three is a feature of many models that describe wind-mediated dispersal (Okubo & Levin 1989). However, despite an apparent high potential for wide-spread, wind-assisted immigration from PNG, in general, *E. flavipes* distribution and abundance as predicted by these models does not agree with the actual distribution and abundance of TS/NPA populations (Chapter three; Anderson *et al.* 2010). Many factors could account for this discrepancy. One of these is the presence of alternate dispersal pathways, such as historic or contemporary human-mediated movement of infested sugarcane among island communities.

If anthropogenic movement of sugarcane does occur, then patterns of movement should be restricted by two quarantine zones which exist between PNG and mainland Australia. These zones have been established in a bid to halt the movement of pests and diseases that could damage Australia's animal and plant industries (Australian Government Department of Foreign Affairs and Trade 1985). Movement of 'declared' items is permitted within PNG, the Torres Strait Protected Zone, the Special Quarantine

Zone, and mainland Australia, but not between zones (Fig. 5-1). Sugarcane is a declared item, so effectively there should be no anthropogenic movement of sugarcane between quarantine zones.

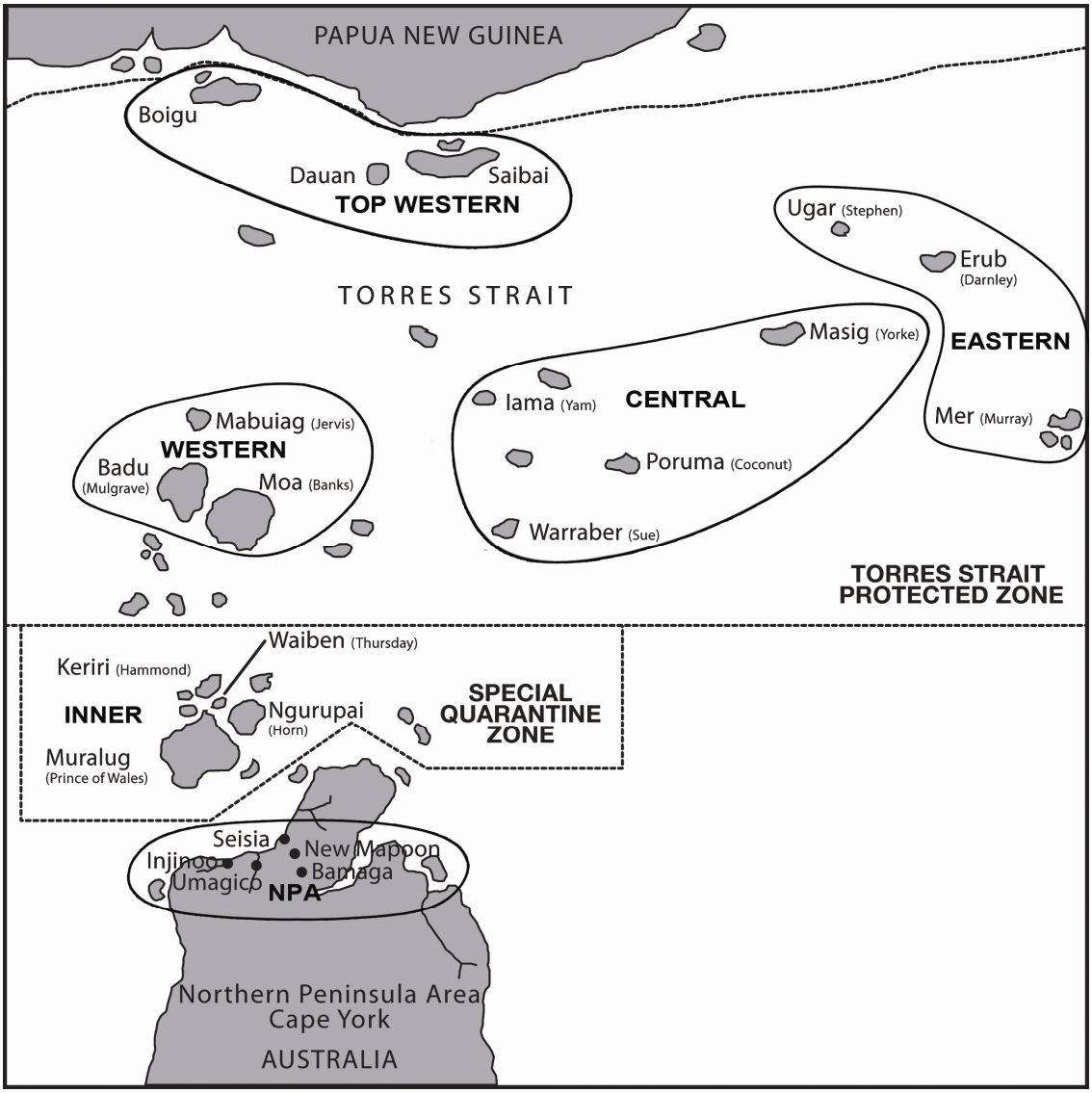


Figure 5-1. Map of the southern coast of Papua New Guinea, Torres Strait islands and Northern Peninsula Area of north Queensland, Australia. Quarantine delimitations of the Torres Strait Protected Zone and the Special Quarantine Zone boundaries are delimited by the dotted lines. Islands are also shown by cultural group, being Top Western, Western, Central, Eastern, Inner, NPA (northern peninsula area).

In this chapter, microsatellite genetic marker systems are used to evaluate both large and small-scale population genetic differentiation and connectivity within and among island and mainland populations of *E. flavipes* throughout the TS/NPA. The

primary hypothesis is that *E. flavipes* most important method of transport into the TS/NPA is long-distance, wind-assisted dispersal from PNG. If so, populations across the TS/NPA should show a decrease in genetic diversity and connectivity with distance from PNG source populations, associated with fewer immigrants reaching peripheral sites (Austerlitz et al. 1997). In the most southern populations, this is likely to produce population growth from matings among limited numbers of colonists, and then their offspring. Thus, these populations should exhibit family-associated genetic structuring and limited connectivity to other sites, especially at locations distance from putative PNG source populations. Exceptions may suggest that alternate dispersal pathways are operating. Therefore, specific tests for population genetic structuring within and among quarantine zones are conducted.

5.2 MATERIALS AND METHODS

5.2.1 *E. flavipes sampling*

In 2006 and 2008, *E. flavipes* were collected from *S. officinarum* and *S.* 'hybrids' at 17 TS and five NPA locations (see chapter four for detailed collection methodology). Individuals sampled from a single host patch were defined as a population, thus 31 populations were sampled (Table 5-1). Host patch size ranged from a single plant with a single stalk, to multiple, inter-twined plants with hundreds of touching stalks and leaves. To limit the likelihood of sampling only related individuals, or under-sampling which could lead to biased allele frequencies (Lowe *et al.* 2004), equivalent numbers of individuals were collected from five randomly selected stalks located throughout each patch. Ideally, samples comprised 25 individuals per patch (five individuals from each of the five randomly selected stalks), but ultimately sample sizes per patch ranged from nine to 27 individuals. If less than 25 individuals were available on the five focal stalks, then where population and patch size permitted additional samples were randomly collected from other stalks within the patch. Samples were transferred immediately to 100 % ethanol. Representative sub-samples of adults were submitted to Delphacidae taxonomist, G. A. Bellis, Darwin, Australia to confirm morphological identification. Voucher specimens from Bamaga, New Mapoon,

Badu and Saibai Islands were lodged with the Queensland Museum, Brisbane, Australia.

5.2.2 *DNA methods and microsatellite characteristics*

To quantify genetic structure in *E. flavipes*, whole insects were sent to the Australian Genome Research Facility Limited for DNA extraction, PCR amplification and microsatellite genotyping at eight polymorphic loci, which have not previously been reported (Table 5-2). For PCR, the initial denaturing step was at 94^0C for 5 min, 35 amplification cycles of 94^0C for 30 s, annealing temperature (Table 5-2) for 45 s, and 1 min of extension at 72^0C, with a final extension at 72^0C for 3 min, with samples held at 4^0C. Applied Biosystems 3730 DNA Analyser platform was used for genetic analysis. GeneMapper 4.1 software (Applied Biosystems) was used for scoring alleles. Microsatellite and primer sequences were submitted to Genbank (Loci and respective Genbank accession number: 1-TER-327 JN565018; 2-TER-427 JN565019; 3-TER-527 JN565020; 4-TER-627 JN565021; 5-TER-727 JN565022; 6-TER-827 JN565023; 7-TER-1027 565024; 8-TER-10 JN565025).

The presence of null alleles, scoring error due to stuttering and large allele dropout were tested with Microchecker 2.2.3 (Van Oosterhout *et al.* 2004). Cervus 3.0.3 (Kalinowski *et al.* 2007) was used to estimate the frequency of null alleles per locus. Linkage disequilibrium (LD) was analysed using the likelihood ratio test, with 10, 000 permutations in Arlequin 3.5.1.2 (Excoffier *et al.* 2005).

Table 5-1. Torres Strait island and northern peninsula area of mainland Queensland, Australia sampling locations by cultural island grouping and sampling year.

Traditional group	Location	Population	Year	GPS co-ordinates	
NPA	Bamaga	1	2006	10°53’37.97”S	142°23’20.82”E
		2	2006	10°53’22.48”S	142°23’24.92”E
		3	2008	10°53’37.97”S	142°23’20.82”E
		4	2008	10°53’22.48”S	142°23’24.92”E
	New Mapoon	1	2006	10°52’10.56”S	142°23’0.35”E
		2	2006	10°52’17.37”S	142°23’8.04”E
Inner	Keriri	1	2008	10°33’12.83”S	142°13’2.11”E
	Waiben	1	2006	10°34’55.69”S	142°13’19.49”E
	Ngurupai	1	2006	10°35’43.82”S	142°14’57.39”E
		2	2006	10°35’34.85”S	142°14’53.96”E
		3	2008	10°35’38.99”S	142°14’56.96”E
Central	Masig	1	2006	9°45’0.40”S	143°24’52.21”E
		2	2006	9°45’1.71”S	143°24’46.76”E
		3	2006	9°45’5.83”S	143°24’38.94”E
Western	Mabuiag	1	2006	9°57’10.26”S	142°11’32.01”E
		2	2008	9°57’25.00”S	142°11’13.73”E
		3	2008	9°57’25.43”S	142°11’13.23”E
	Badu	1	2006	10° 9’1.03”S	142°10’12.33”E
		2	2006	10° 9’0.17”S	142°10’13.14”E
		3	2008	10° 9’20.35”S	142°10’6.00”E
Top Western	Dauan	1	2006	9°25’8.19”S	142°32’29.68”E
		2	2008	9°25’7.01”S	142°31’46.87”E
		3	2008	9°25’8.19”S	142°32’29.68”E
	Saibai	1	2006	9°22’54.07”S	142°36’42.39”E
		2	2006	9°22’37.29”S	142°37’32.80”E
		3	2008	9°22’52.12”S	142°36’40.99”E
		4	2008	9°22’34.08”S	142°37’25.68”E
	Boigu	1	2006	9°13’48.63”S	142°13’8.68”E
		2	2006	9°13’50.22”S	142°13’11.74”E
		3	2008	9°13’51.81”S	142°13’13.38”E
		4	2008	9°13’48.93”S	142°13’16.05”E

Table 5-2. Annealing temperature ^{0}C (T_a), cloned allele size (CAS), total number of alleles (A), inbreeding coefficient (F_{IS} - asterisk (*) indicates significance at P = 0.05), per loci for eight pairs of novel *E. flavipes* microsatellite primers.

Locus	Sequence (5'–3')	Repeat	CAS	T_a	A	F_{IS}
8-TER-10	F TTTGCTGTCAACTCCCATTG R GATGAGAGATGACAAGA	$(AC)_3$ $(AC)_{24}$	189	55	25	-0.0252
1-TER-327	F TGAGGCGTGGCTGCTAGT R CATTTCCATTAGTAATTTTCCCTCA	$(AC)_{16}$	164	52	23	0.1451*
2-TER-427	F TCATTTCAGCAAATTGTGAGC R CCCTATGATCACTTAGCAACCA	$(AC)_{11}(AC)_9$	135	52	15	-0.0189
3-TER-527	F GGAATACTGGGTGTGAGTTGC R AATGAGGCCGACTTGTATGC	$(CA)_7$ $(CA)_7$	170	55	45	-0.0415
4-TER-627	F GCTCACGTTCAAGCTTCCTC R GAGGGGAGAGGGAGTGAGAG	$(CA)_{10}$	195	55	24	-0.0539
5-TER-727	F TGCATGGGTAATGAAGTGGA R GTAATGGACGGGCTACAGGA	$(CA)_6(CA)_7$ $(CA)_{11}$	202	52	28	0.0057
6-TER-827	F GCCTGGCACTCACATACACA R TCACTAGCTTGCAGTTTGCTG	$(CA)_{16}$	122	52	17	0.4747*
7-TER-1027	F TTCTGGCATACTGGGTGTGA R CCGGCAGATAGGAGTTTGAG	$(CA)_3(CA)_6$	153	52	9	-0.1334

5.2.3 ***Population genetic variability***

Population genetic characterisation was done by calculating the expected (H_E) and observed heterozygosity (H_O). Locus by locus departure from Hardy-Weinberg equilibrium (HWE) was tested by determining significance of the inbreeding coefficient F_{IS} (heterozygosity deficit), with 10, 000 permutations in Arlequin. Allelic richness is an important measure of genetic diversity (Petit *et al.* 1998), and so was used in this study. As allelic richness is highly dependent on sample size, the data was standardised using rarefaction, in the program HP-RARE v June-6-2006 (Kalinowski 2005). The standard sample size chosen was nine individuals, which was the smallest sample size per population obtained. All multiple comparison *P* values were corrected for false discovery rate (FDR), which controls the proportion of significant results that are false positives (type I errors) (Benjamini & Hochberg 1995).

5.2.4 *Population connectivity and genetic structure*

To ensure that F-statistics, which measure population differentiation based on allele identity, are an appropriate measure of population genetic differentiation for this data, as opposed to R_{ST} which is an allele size-based measure of differentiation that assumes a stepwise mutation process, the test described in Hardy *et al*. (2003) was used. The multilocus R_{ST} value was not significantly higher than the mean pR_{ST} ($P = 0.564$). The allele size permutation tests therefore do not reveal any significant contribution of stepwise mutations to population differentiation; therefore F_{ST} is a suitable statistic for use.

Isolation by distance was examined in the first instance to test the standard theory of increasing genetic differentiation with geographical distance (Wright 1943), and to obtain a preliminary estimate of the magnitude of inter-population gene flow throughout the TS/NPA. A Mantel test was conducted with pairwise Slatkin's linearised F_{ST} $[F_{ST}/(1-F_{ST})]$ and the natural log of pairwise geographic distances (Rousset 1997). Significance was assessed with 9999 permutations in Arlequin. To calculate the geographic distances, latitude and longitude co-ordinates recorded in the TS/NPA on a Garmin GPS 60 device were uploaded to Google Earth 5.1.3533.1731 (Google Inc. 2009). Distances between sampling locations were calculated using the Google Earth ruler tool at 'eye view' 1 km above the ground for consistency.

To examine the applicability of the "wind-immigration hypothesis", regression analyses were used to test for an effect of isolation by distance from known *E. flavipes* infestations along the southern coast of PNG. *E. flavipes* has been recorded on sugarcane grown in the southern coastal PNG villages of Sigabaduru, Mabaduan, Daru and Buzi on many occasions (Waterhouse *et al.* 1995; Grimshaw 1999; Magarey *et al.* 2002). In fact, *E. flavipes* is so common in these villages that Australian Quarantine and Inspection Service (AQIS) scientists rarely collect it during routine plant health surveys, instead just noting its continued presence (Grimshaw, J. F. 2007, *pers. comm.*). GPS co-ordinates for each of these four potential source populations are recorded during AQIS plant health surveys. The PNG co-ordinates along with GPS co-ordinates for each sampled TS/NPA infestation, were uploaded to Google Earth. Distances between each TS/NPA population and the closest PNG village infestation were

measured using the Google Earth ruler tool, as described previously. These distances were used as the predictor variable in the regression analyses.

Foll and Gaggiotti (2006) recommended population specific F_{ST} as particularly useful for estimating the genetic uniqueness of individual populations within a group of populations when used in conjunction with allelic richness as a measure of genetic diversity (Gaggiotti & Foll 2010). Mean population F_{ST} was calculated in the program Geste (Foll & Gaggiotti 2006), and used along with allelic richness (A_R), and the multilocus inbreeding coefficient (F_{IS}), as dependent variables in the linear regression analyses.

Overall genetic differentiation throughout the TS/NPA was assessed with F_{ST} (Wright 1965) using analysis of molecular variance (AMOVA). Despite the assumptions of F_{ST} often being violated in natural populations, it remains useful in describing population structure (Pearse & Crandall 2004). Spatial hierarchical AMOVA was used to test whether significant genetic differentiation occurred between quarantine zones within the TS/NPA. Populations were grouped as follows: (i) mainland Australia (NPA) (Bamaga and New Mapoon), (ii) Special Quarantine Zone (SQZ) (Keriri, Waiben and Ngurupai), and (iii) Torres Strait Protected Zone (TSPZ) (Masig, Mabuiag, Badu, Dauan, Saibai and Boigu). In all cases, significance of *P* values was assessed with 10, 000 permutations in Arlequin.

In addition to classic F_{ST} analyses, clustering methods provide good evidence for inferring population structure (Estoup *et al.* 2010). The Bayesian clustering method implemented in Structure v 2.2.3 (Falush *et al.* 2003) was used to test for evidence of population genetic structuring, assign individuals to populations and to identify admixed individuals (Falush *et al.* 2003). Although Structure supposedly assumes that all potential source populations have been sampled when assigning individuals, as opposed to alternate assignment methods such as Geneclass2 (Piry *et al.* 2004), Rollins *et al.* (2009) found that results using either method were in general agreement. In any event, there are no inferences made regarding the origin of specific individuals, instead discussion concentrates on broader patterns. Also, Structure assumes that within populations, loci are in HWE (Pritchard *et al.* 2000), but violation of this assumption does not appear to significantly affect Structure results (De Barro 2005; Brown *et al.* 2011). As the number of genetic clusters (*K*) in the data was unknown, Structure was used to assign individuals into the most likely *K*. Results for $K = 1$ to $K = 33$ were evaluated, being no genetic structure at all ($K = 1$) to every sampled population being

genetically distinct (K = 31). Estimates of K were based on 10 iterations, each with a burn in of 50 000, and Markov Chain Monte Carlo (MCMC) lengths of 100 000 using the admixture model and correlated allele frequencies. The optimal value of K was based on both log probabilities [Pr (X|K)] and ΔK, which may provide a more realistic value of K (Evanno *et al.* 2005). Summary outputs were viewed in Structure harvester v 0.6.1 (Earl 2011). Structure assigns each individual to a cluster based on the value of Q, or the proportions of an individual's genome that originated from K populations (Pritchard *et al.* 2000). Individual assignment to a particular cluster was based on the largest average proportion of their genotype assigned to a cluster over the 10 iterations.

As per the hypothesis that there will be related individuals within populations, a maximum-likelihood model, Colony v 2.0.1.1 (Jones & Wang 2010), was used to analyse specifically for genealogical relationships within and between populations, by reconstructing sibling relationships (sib-ships). Colony employs a group-likelihood approach using MCMC procedures, where all individuals in the entire sample are considered simultaneously and partitioned into distinctive genetic groups that maximise the likelihood of the proposed family relationship (Jones & Wang 2010). Colony is also able to account for genotyping errors (Jones & Wang 2010). Individuals (n = 648, 7 loci) were pooled, and an allelic dropout rate of 0.1 %, and 1.5 % for other errors were assumed. Female monogamy and male polygamy were selected because it appears unlikely that female planthoppers mate repeatedly, whereas multiple mating by males is common (Claridge & Vrijer 1994). Three long and three medium runs were conducted, each with different random seed numbers. Results were tested for convergence by plotting the change in Log-likelihood as a function of the number of iterations (Jones & Wang 2010), and only inferred sib-ships with a probability over 0.9 were plotted.

Input files were formatted using Convert 1.31 (Glaubitz 2004), Microsatellite Toolkit (Park 2001), Genalex (Peakall & Smouse 2006) and PGDSpider 2.0.0.2 (download from http://heidi.chnebu.ch/doku.php?id=pgdspider).

5.3 RESULTS

5.3.1 *Microsatellite characteristics, Hardy-Weinberg Equilibrium and Linkage Disequilibrium*

A total of 648 individuals from 31 populations were sampled throughout the TS/NPA. All eight loci were polymorphic, with a total of 186 alleles. No scoring errors or allele drop-out were detected. F_{IS} values at Loci 1-TER-327 and 6-TER-827 were significant (Table 5-2). However, the F_{IS} value at 1-TER-327 was closer to the range of F_{IS} values at other loci, except for 6-TER-827 (see below). Analyses run with and without 1-TER-327 did not change any significance outcomes, so this locus was included in all analyses to increase statistical power.

The F_{IS} value at 6-TER-827 was an order of magnitude larger than that of other loci (Table 5-2). Further, 77% of populations showed significant deviation from HWE at this locus, and Microchecker indicated it was likely due to the presence of a null allele. Cervus estimated the frequency of null alleles at 6-TER-827 to be 0.52. Consequently this locus was excluded from all further analyses. For the remaining seven loci, significant HWE deviation occurred at five of seven and six of seven loci at Keriri1, Mabuiag1 and Dauan2, respectively (Appendix 1). However, there was no significant global deficit of heterozygotes in those populations (multilocus population F_{IS} values not significantly different from zero) (supporting information 1). Isolation by distance calculations were conducted with and without these three populations. In no instance did their inclusion alter result significance, so results presented include all populations.

Significant LD occurred in most populations after FDR correction (Appendix 1). This result was expected, given that some sampled populations may have been influenced by processes such as founder effects and inbreeding, which are known to cause LD (Slatkin 2008). Importantly, no loci were consistently linked across multiple populations, so it was assumed loci assorted independently for statistical testing.

AMOVA was used to determine if different host types and/or sampling at different times caused genetic substructure at single locations (Balloux & Lugon-Moulin 2002). All samples bar one were collected from patches consisting of only one host type, except at New Mapoon1, where samples were taken from a single host patch which consisted of both *S. officinarum* and *S* 'hybrids'. No significant genetic structuring by host type was observed (AMOVA, F_{ST} = -0.02, P = 0.54) at this location, so these samples were pooled. Similarly, the same host patches at Bamaga and Dauan

were sampled in 2006 and 2008, but were coded separately as Bamaga1 and Bamaga3, Bamaga2 and Bamaga4, and Dauan1 and Dauan3, respectively. These samples were treated at separate populations in later analyses.

5.3.2 *Population connectivity*

Isolation by distance analysis revealed a significant positive correlation between Slatkin's linearised F_{ST} and the natural log of geographic distance (Mantel $r = 0.15$, $P = 0.0003$) (Fig. 5-2). Despite the significance of this relationship, the Mantel r value of 0.15 suggests that geographic distance is a relatively poor predictor of levels of genetic differentiation. High levels of genetic variability were consistently observed between pair-wise Slatkin's linearised F_{ST} values regardless of distance between populations.

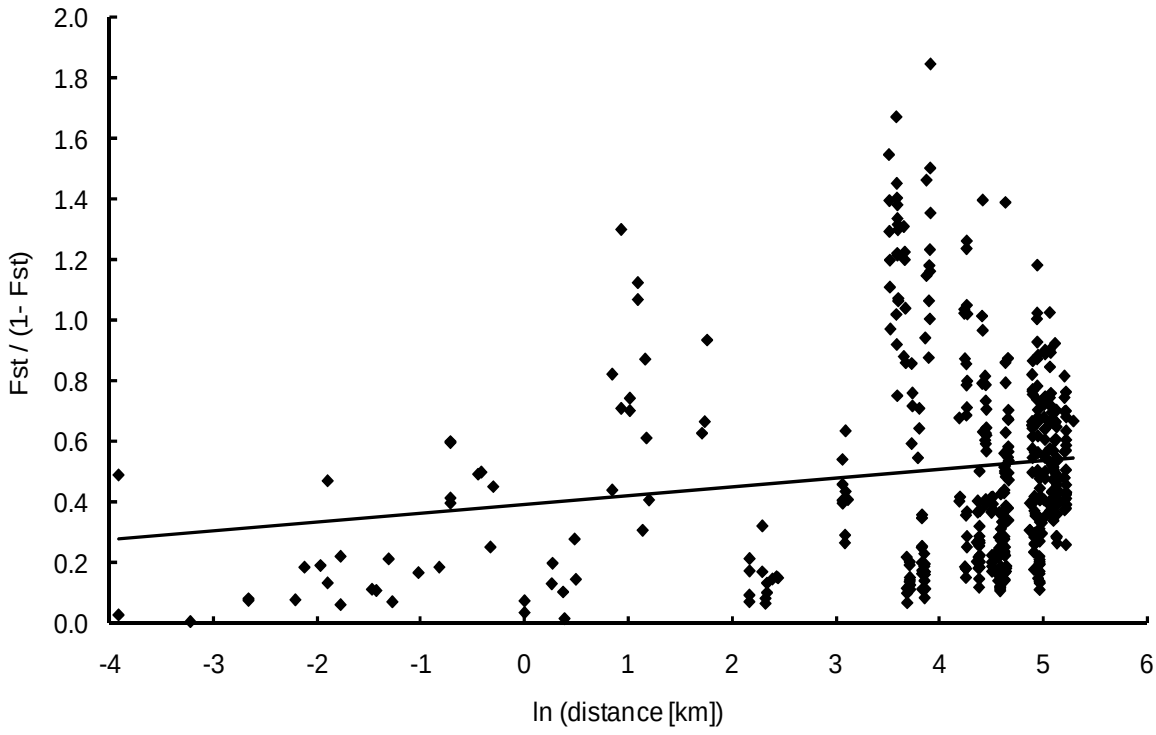
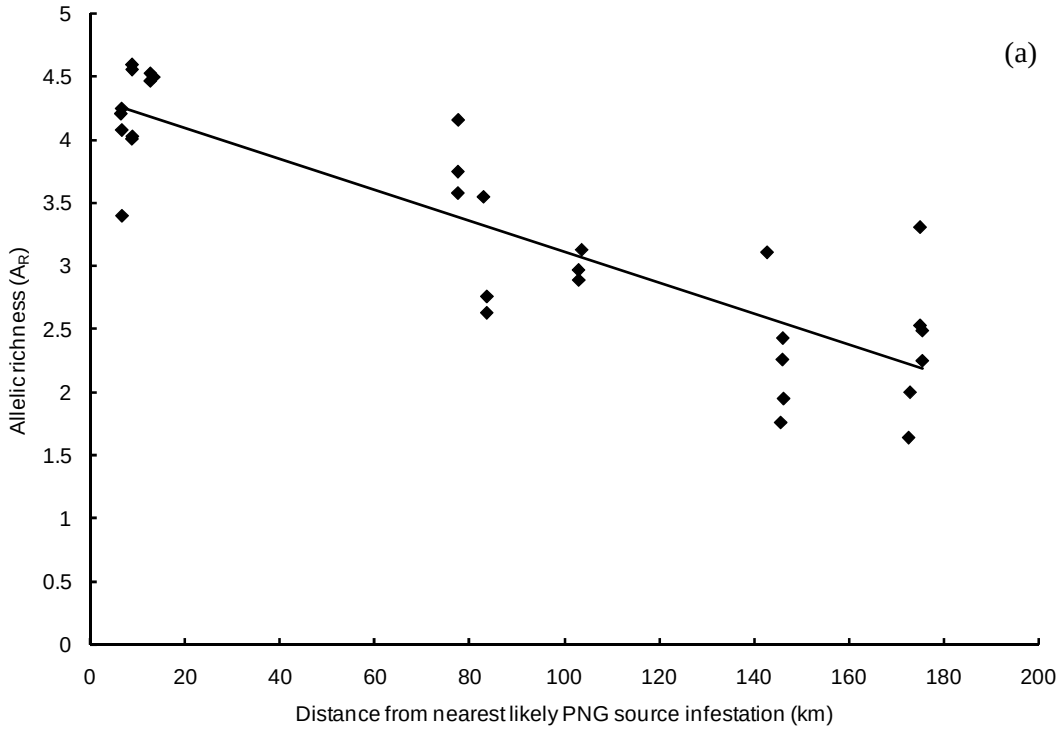


Figure 5-2. Effect of natural log geographic distance on Slatkin's linear genetic distance for *E. flavipes* populations on the Torres Strait islands and northern peninsula area of Australia.

5.3.3 *Factors influencing population genetic diversity and structure*

Mean population allelic richness was significantly negatively related to distance from PNG, with distance explaining 75 % of the variation in allelic richness differences between sites (Adj $R^2 = 0.751$, $F_{1, 29} = 91.566$, $P < 0.001$; Fig. 5-3a). Populations close to PNG were significantly more genetically diverse than populations on the NPA.



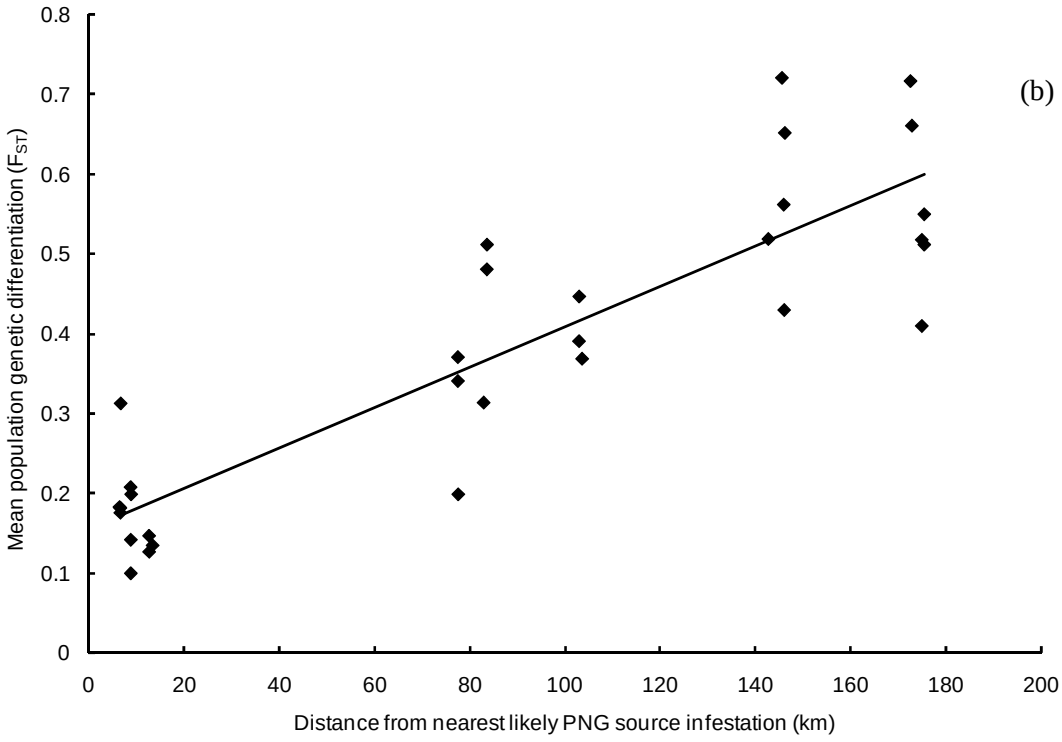


Figure 5-3. Effect of distance from nearest likely *E. flavipes* Papua New Guinea source infestation on (a) mean population allelic richness (A_R), and (b) mean population genetic differentiation (F_{ST}) in the Torres Strait and northern peninsula area of Queensland, Australia.

Mean population F_{ST} throughout the TS/NPA significantly increased with increasing distance from PNG. Distance from PNG alone explained 77 % of the variation in F_{ST} (Adj R^2 = 0.770, $F_{1, 29}$ = 101.38, $P < 0.001$; Fig. 5-3b). Populations close to PNG contributed significantly less to the overall population structure than populations on the NPA. Distance from the nearest likely PNG infestation was not a significant factor in determining the population inbreeding coefficient, suggesting that inbred populations occur throughout the TS/NPA (Adj R^2 = -0.005, $F_{1, 29}$ = 0.863, P = 0.361).

5.3.4 *AMOVA, Structure and Colony*

A global F_{ST} of 0.32 ($P < 0.001$) suggests that significant population genetic differentiation occurs throughout the TS/NPA. Of the total variation, 68 % occurred within populations, with the remaining 32 % variation among populations also

significant. After FDR correction, 463 of the 465 population pair-wise F_{ST} comparisons were significant. Only Badu1 and Badu2 (both sampled 2006) and Saibai3 and Saibai4 (both sampled 2008) were not significantly different from each other (pair-wise F_{ST} = 0.004, P = 0.29, pair-wise F_{ST} = 0.014, P = 0.07, respectively). Results of the hierarchical AMOVA indicated significant regional structuring also occurs, where 16.6% of the overall variation was attributed to quarantine zone. However, only 20.06% variation occurs among populations within quarantine zones which is low when compared to the 63.34% of variation that occurs within populations (F_{ST} = 0.37; F_{SC} = 0.24, F_{CT} = 0.17; $P < 0.001$). So although significant, grouping populations by quarantine zone only weakly explains population genetic structuring in the TS/NPA. The majority of genetic differentiation is explained at the individual population level.

Structure analyses indicated the highest average log likelihood over 10 runs occurred at K = 26 (-11745.70) (Fig. 5-4). Using the Evanno method (Evanno *et al.* 2005), the ΔK statistic peaked at K = 26 (3.93) (Fig. 5-4). These results support those of the AMOVA, which suggest that strong population structuring occurs in the TS/NPA.

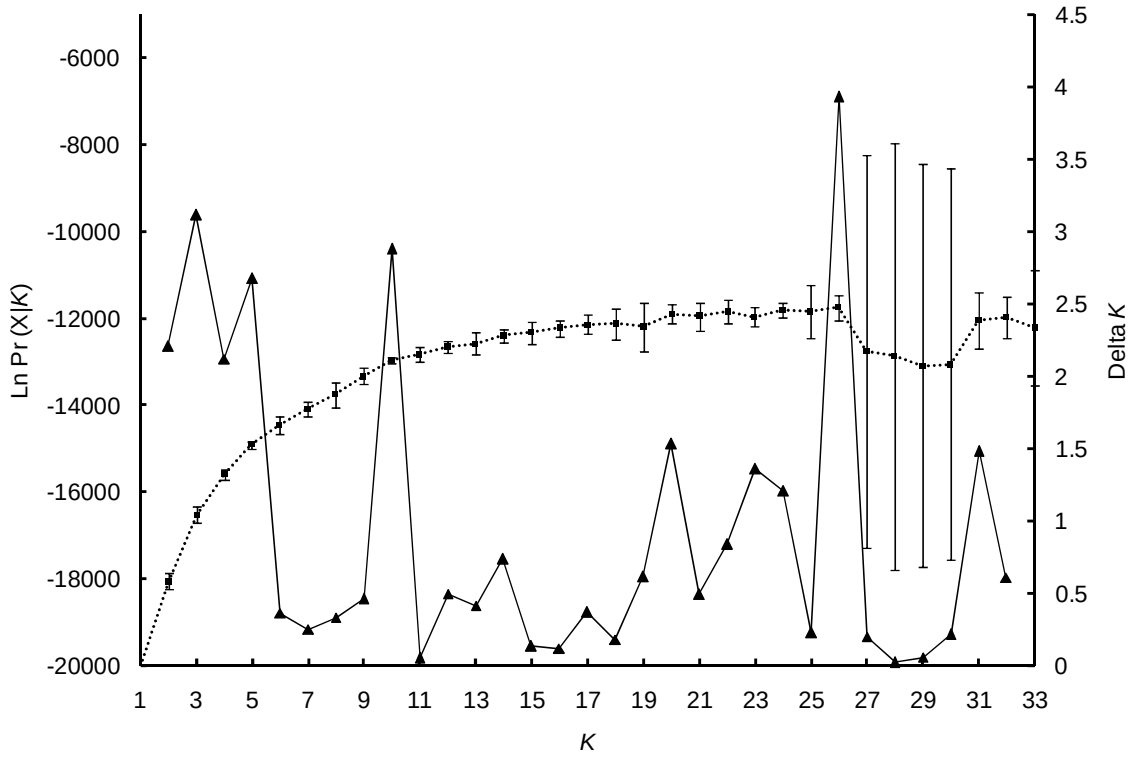


Figure 5-4. Results of Structure cluster analysis for K = 1 – 33 *E. flavipes* populations sampled throughout the Torres Strait islands and northern peninsula area of Australia, showing average log likelihood LnPr (X|K) on the primary axis, with ΔK values on the secondary axis.

Close examination of *K* = 26 revealed three general patterns (Fig. 5-5a). First, each of eight clusters contained either all the individuals sampled from a single population, or all the individuals sampled from certain groups of populations. The majority of populations in these clusters are in the southern TS and on the NPA. For example, all individuals sampled from Waiben1 and all three Ngurupai populations formed a single cluster (Fig. 5-5a). Second, four clusters contained 100% (or close to) of the individuals sampled from a single population/s, as well as individuals sampled from more northerly locations in the TS/NPA. In support of the AMOVA pair-wise comparison result, Structure assigned 96% of the individuals sampled from Badu1 and 100% from Badu2 to a single cluster, which also included a number of individuals sampled from Saibai1-4. Finally, the remaining clusters contained a mix of individuals sampled from a number of islands close to the coast of PNG. These clusters occasionally included an individual sampled from a population further south. A clear

pattern to note is that the proportion of admixed individuals within populations decreases with distance from PNG (Fig. 5-5a).

The ΔK statistic also suggested that broader structuring occurs, with peaks at K = 3 (3.11) and K = 10 (2.88) (Fig 5-4). A reasonable biological explanation was not apparent for K = 10, but K = 3 was examined to determine if the clusters contained populations grouped according to quarantine zone, which they did (Fig. 5-5b).

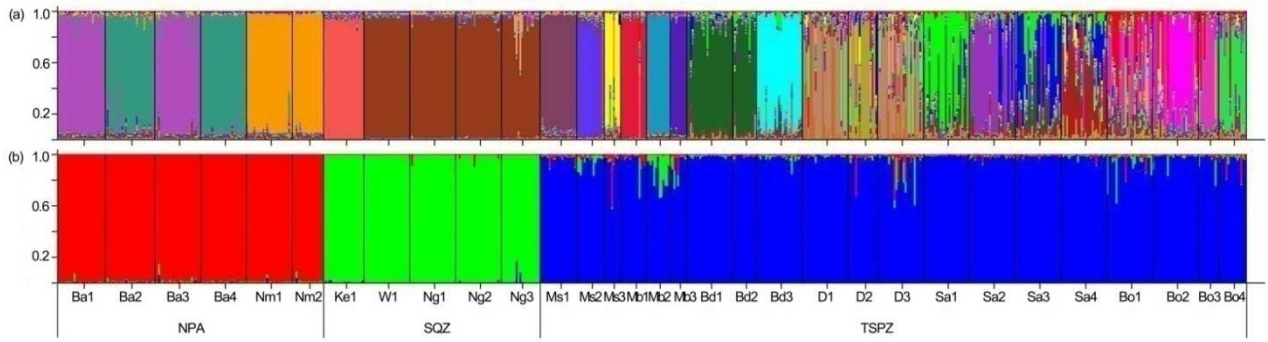


Figure 5-5. Structure *Q* plots to estimate the number of genetic groups (*K*) present across the Torres Strait and northern peninsula area of Queensland, Australia. Each plot is presented in population order, coded as follows: Bamaga (Ba), New Mapoon (Nm), Keriri (Ke), Ngurupai (Ng), Masig (Ms), Mabuiag (Mb), Badu (Bd), Dauan (D), Saibai (Sa), Boigu (Bo), and grouped by quarantine zone: northern peninsula area (NPA), the Special Quarantine Zone (SQZ), Torres Strait Protected Zone (TSPZ). Each sampled individual is represented by a vertical bar showing the degree of admixture, where (a) results for K = 26; (b) results for K = 3.

The Colony analyses suggested significant family structure throughout the TS/NPA; a total of 10, 845 dyads (4554 full-sib and 6291 half-sib) with a probability over 0.9 occurred. Plots of the change in Log-likelihood values as a function of the number of iterations from each of the replicate runs were consistent, indicating that the annealing procedure produced convergence and was powerful (Jones & Wang 2010). Individuals were assigned to their correct sampling location close to the Australian mainland, suggesting a high degree of reliability in the overall assignments (Fig. 5-6).

Figure six graphically depicts the distribution of family structure throughout the TS/NPA. A ‘mosaic’ sib-ship pattern between Bamaga1-3 and Bamaga2-4 (and to a

lesser extent Dauan1-3) likely reflects common ancestry over time, as each population pair were on the same plants sampled in two different years. Colony suggests the presence of only full-sibs at Mabuiag1 and Mabuiag2. The sib-ship pattern surrounding Boigu, Saibai and Dauan, close to the coast of PNG, appears 'scattered' as a result of sib-ships between multiple populations and locations (Fig. 5-6). Although not the dominant sib-ship pattern, this effect extends to Badu. In contrast, the pattern of sib-ships appears 'linear' for the remaining islands as a result of sib-ships occurring between individuals within a single population, or to a lesser extent either between populations within a single location. For example, individuals sampled from Bamaga, New Mapoon and Hammond do not appear to be connected to populations at other locations; this pattern agrees with the Structure clustering at $K = 26$. Many individuals sampled from Waiben and Ngurupai are related at either half or full-sib level, which are geographically 'next door'.

Pair-wise comparisons suggests two individuals from Waiben1 (sampled 2006, negative for live adults in 2008) were full-sibs to the majority of individuals at Ngurupai3 (plants not present 2006, sampled 2008), and that many individuals between the two locations were related at half-sib level. When asked during the survey, the owner of the sugarcane plants at Ngurupai3 said she had sourced the plants from Waiben1. Similar linear sib-ships occur across New Mapoon1 and 2, Waiben1 and Ngurupai1 and 2, as well as between Ngurupai1, 2 and 3. Further examples of directional across-location sib-ships are evident between Badu1 and 2 and Saibai1, 2 and 3, where a number of individuals from Saibai are related at both full and half-sib level to the majority of individuals at Badu1 and 2.

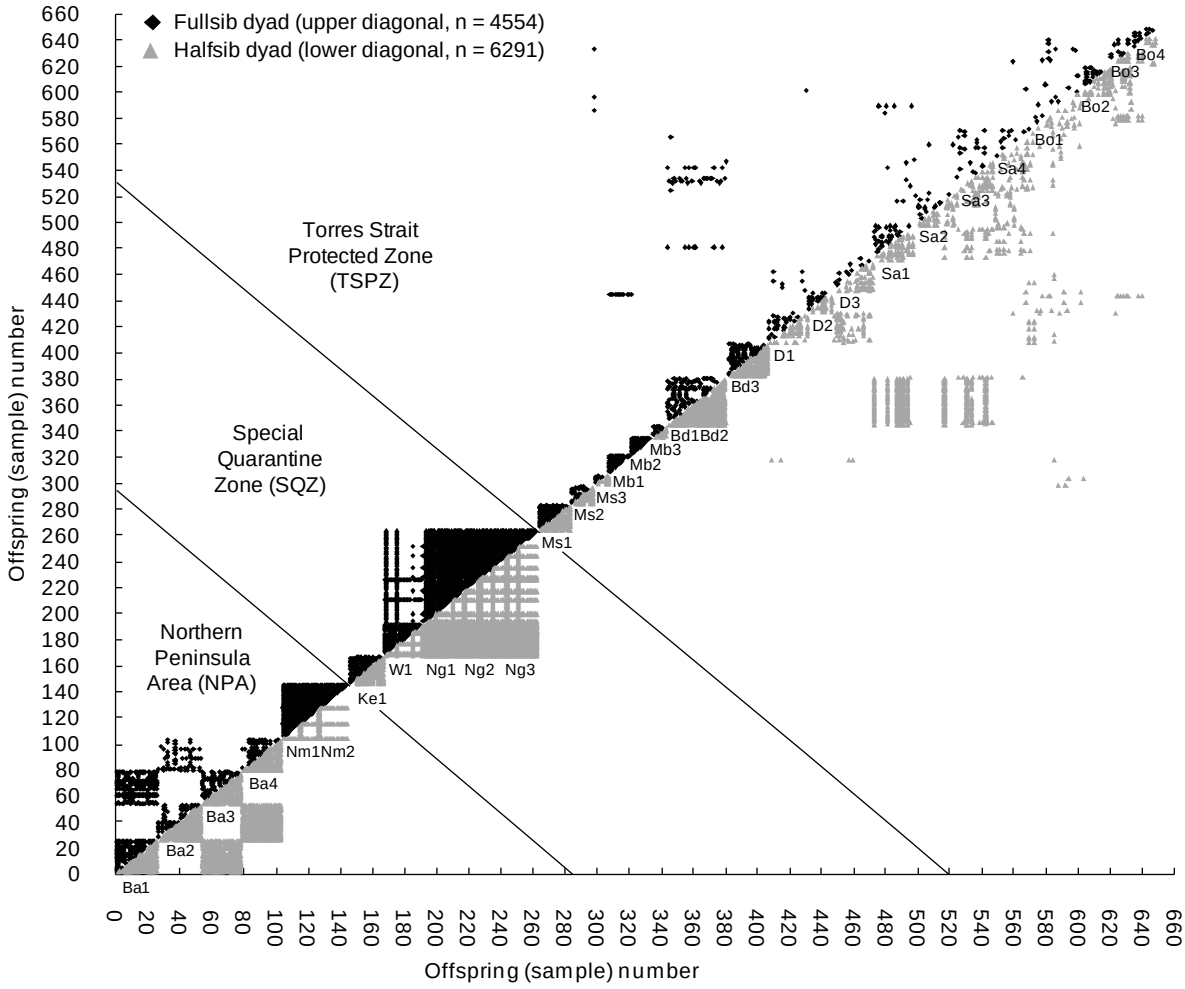


Figure 5-6. Plot from Colony program of "best (maximum likelihood) sibship assignment", showing pair-wise full-sib and half-sib relationships among sampled individuals (offspring number equals sample number, x- and y-axes numbered 1 - 648) within and between populations in the Torres Strait and northern peninsula area of north Queensland, Australia. The graph is divided into differing quarantine regions, being the northern peninsula area (NPA), the Special Quarantine Zone (SQZ) and the Torres Strait Protected Zone (TSPZ). Population codes are: Bamaga (Ba), New Mapoon (Nm), Keriri (Ke), Ngurupai (Ng), Masig (Ms), Mabuiag (Mb), Badu (Bd), Dauan (D), Saibai (Sa), Boigu (Bo).

5.4 DISCUSSION

In this chapter, genetic variation of the island sugarcane planthopper, *Eumetopina flavipes*, throughout the island archipelago of the Torres Strait was analysed. In keeping with previous trajectory modelling for *E. flavipes* (Chapter four; Anderson *et al.* 2010), and commonly used dispersal curves for wind-immigration that predict fewer immigrants at the range extreme (Okubo & Levin 1989), we predicted that distance from PNG would affect the magnitude and rate of wind-assisted immigration into the TS/NPA. The primary hypothesis that long-distance, wind-assisted dispersal from PNG drives *E. flavipes* invasion into the TS/NPA is supported by the findings of this chapter.

A significant isolation by distance effect across the Torres Strait suggests that at the macro-scale, geographic distance does have some influence on gene flow between populations within the TS/NPA. However, levels of genetic variation also clearly demonstrate that populations only four metres apart can be as genetically distinct as populations 100 km apart. This variation likely contributes to the relatively poor fit of the isolation by distance model, which clearly does not conform to expectations under a stepping-stone scenario where gene flow occurs only between neighbouring populations (Kimura & Weiss 1964). It is expected that various historical and ecological factors will alter patterns expected under isolation by distance, and violate the assumption of regional equilibrium (Hutchison & Templeton 1999). For example, a classic isolation by distance effect can be tempered by continual re-introductions via long-distance dispersal from a source (Ramakrishnan *et al.* 2010).

Populations on Boigu, Saibai and Dauan islands which are geographically adjacent to the PNG coast-line, exhibit significantly higher genetic diversity and lower population-specific genetic structuring than populations closer to and on mainland Australia. This indirect evidence suggests that distance from PNG, rather than the classic isolation by distance expectation, better explains the population genetic variation and structure observed through the TS/NPA. Such alternate distance measures often do better explain genetic differentiation because they account for the impact of alternate features on gene flow (Lowe *et al.* 2004; Storfer *et al.* 2007).

High levels of within population genetic diversity as well as admixture, as observed close to PNG, are commonly attributed to multiple independent introductions from a number of genetically diverse source populations (Allendorf & Lundquist 2003;

Kolbe *et al.* 2004; Chu *et al.* 2011) or a single large introduction from a highly diverse source (Colautti *et al.* 2005). Large, seasonal founding events by multiple individuals from PNG, as promoted by wind could thus explain the general trends in our results. The apparently random assignment of individuals to clusters by Structure, and the dominant 'scattered' pattern of inter-population relationships observed between northern populations also fits with a model of general random distribution of founder populations, which appears the norm for long-distance planthopper migrants (Perfect & Cook 1994).

In contrast, populations in the southern Torres Strait and on mainland Australia exhibit low levels of population genetic diversity and increasing genetic structuring. Combined, these characteristics suggest that populations in the southern TS and NPA are founded via increasingly rare immigration events by relatively fewer individuals than populations close to PNG, as would be expected at these distant locations under the wind immigration scenario. Lower relative genetic variation in introduced populations can be due to a severe bottleneck caused by limited founders from limited sources (Lowe *et al.* 2004; Colautti *et al.* 2005). Progressive range expansion where populations are colonised one after the other in a linear stepping-stone model of colonisation, can produce a decrease in genetic diversity along the range (Excoffier *et al.* 2009), and there may be a small element of secondary movement contributing to the significant isolation by distance relationship. However, pair-wise comparisons and Structure results show almost all sampled populations are genetically distinct, independent aggregations, so a north to south, progressive 'island-hop' mode of dispersal is not consistently supported by results.

Results from a number of studies that compare prevailing wind direction with population genetic data support the findings of this chapter. Analysis of the brown planthopper *Nilaparvata lugens* (Stål) mtDNA showed higher haplotype diversity in northern populations was consistent with a seasonal, northward migration from south-eastern China to Korea, as predicted by weather patterns (Mun *et al.* 1999). A similar study was conducted on white backed planthopper *Sogatella furcifera* (Horvath) ISSR markers. Significant genetic differentiation between sampled regions, and patterns of population clustering suggested that northern *S. furcifera* migrated from a number of southern locations (Liu *et al.* 2010). *Bemisia tabaci* (Gennadius) microsatellite data suggest that in Australia, two main north and south populations occur with high levels of gene flow between them. The levels of admixture within the two populations suggest

south to north movements, which reflect prevailing wind trajectories at a time of year when the whiteflies are most active (De Barro 2005).

Significant genetic heterogeneity is clearly evident throughout the entire region (F_{ST} = 0.32), suggesting that gene flow following colonisation is limited. Bayesian modelling also indicated high levels of genetic structuring, and Colony results suggested that the relative level of differentiation is due to aggregations of related individuals within populations. The aggregations appear particularly evident on the NPA. A 'colonisation syndrome' has been described for migrating planthoppers, where initial colonisation densities may be low but rapid population growth quickly occurs (Kuno 1979). Dispersal limitation within host patches was shown for the planthopper *Delaphacodes scolochloa* (Cronin 2009), and for other planthopper species, low dispersal by nymphs and some adults result in strong aggregations on host plants (Perfect & Cook 1994). Such aggregations may lead to higher levels of inbreeding, where small populations could consist of a single family of full-sibs (Orsini *et al.* 2008), or even subpopulations of family groups which persist into older, more established populations (Giles *et al.* 1998). Breeding systems and gene flow are primary drivers of genetic differentiation within populations (Chesser 1991). Results agree qualitatively with the colonisation syndrome described for planthoppers involving limited dispersal post-colonisation. Therefore, it is feasible to suggest that for *E. flavipes*, population growth is kin-structured and serves to enhance relative founder effects through the TS/NPA, ensuring that strong genetic differentiation persists over time.

It is possible the high F_{ST} values are a result of sampling error, such as sampling only related individuals. Distinct efforts were made to sample across entire host patches to avoid this possibility. Although the results were not presented, all samples per island were pooled in the first analyses. Wahlund effects were immediately evident, and the sampling unit was reduced to single host patches. Results likely reflect the reality, in that populations can indeed be composed of related individuals. It is also possible that within a host patch, family groups occur on individual stalks, so that multiple families were sampled.

Significant hierarchical AMOVA and Structure clustering at K = 3 support the hypothesis that secondary movement between and/ or within islands could occur, and appears restricted within quarantine zones. Waiben and all three Ngurupai populations cluster together, and a very tight family relationship exists between these populations. Anecdotally, the sugarcane plants at Ngurupai3, which were not present in 2006, were

sourced from Waiben1. Thus, the linear pattern of sib-ships across these two locations could represent a known, directional movement of infested sugarcane. In support of such movement occurring and resulting in live individuals, a reduced number of individuals survive over time on cut stalks (Chapter two; Anderson *et al.* 2007). Also, cut stalks denuded of all adults and nymphs, but with viable eggs present in the leaf vein can hatch after transplantation (K. L. Anderson, Unpublished data). Although no direct evidence exists to support the occurrence of anthropogenic movement in the TS/NPA, New Mapoon1 and 2 are connected through related individuals, as are Badu1 and 2 to Saibai1 thru 4; these could represent deliberate movements. Although it would be very difficult to catch a person in the act of moving infested sugarcane, experimental transplantation of infested stalks would quantify population genetic patterns resulting from such movement, and add support to results presented here that quarantine zones appear to limit secondary, potentially anthropogenic, movements of *E. flavipes*.

.

CHAPTER 6 GENERAL DISCUSSION

6.1 INTRODUCTION

The overall aim of this thesis was to determine the relative importance of pre- and post invasion processes contributing to the invasion success of the island sugarcane planthopper, *E. flavipes* through the Torres Strait. In chapters two and three, dispersal mechanisms which potentially enable movement to new regions were explored. Chapter four examined the on-island influences of host plant dynamics, which drive colonisation, population growth and persistence, whilst chapter five drew together results from the preceding data chapters using statistical molecular methods. Here, the main findings from each chapter are summarised, and the final recommendations for management of *E. flavipes* in the Torres Strait are outlined.

6.2 ANTHROPOGENIC MOVEMENT OF INFESTED SUGARCANE

Results presented in chapter two clearly indicate that *E. flavipes* males, females and nymphs can survive up to six days on cut sugarcane, albeit providing relatively small colonising populations at the end of that time. The starting population size on each stalk has important ramifications on the numbers of individuals available for colonisation at the end of a transportation event. If the source population was large enough, anthropogenic movement could result in potential colonising individuals being moved to all regions of the TS/NPA.

The cultural history of the Torres Strait appears to have provided ample opportunity for the transportation of sugarcane stalks and *E. flavipes* throughout the region, therefore *E. flavipes* may have been present in the Torres Strait for hundreds of years. Individuals present on a stalk after transportation may also possess an ability to colonise existing sugarcane plants upon introduction, although this remains to be tested.

Both nymph and adult *E. flavipes* are able to vector Ramu stunt disease (Kuniata *et al.* 1994), so this pathway remains a potential introductory route for the disease into Australia. Therefore, human-mediated movement of infested plant material has the potential to be an important component in the dispersal of the island sugarcane planthopper *E. flavipes*.

6.3 LONG-DISTANCE, WIND-ASSISTED IMMIGRATION FROM PNG

Wind may be an important dispersal vector for *E. flavipes* that could allow significant, seasonal incursions into and throughout the TS/NPA. Islands close to PNG appear at high risk of immigration via wind-assisted dispersal, whereas results suggest wind may contribute to recolonisation at other locations throughout the TS/NPA but at a lower frequency. In addition, simulations showed that long-range movement could be in the order of hundreds of kilometres; if this were true then insects could potentially be transported to commercial sugarcane growing regions near Cairns, Australia.

However, the general discrepancy between patterns of infestation as predicted by wind-assisted immigration and observed infestation supports the hypothesis that alternative factors are more important than levels of immigration as promoted by wind in determining the overall invasion success of *E. flavipes* in the Torres Strait.

This is the first study to model patterns of wind-assisted immigration of an invasive pest species from PNG, and associate such immigration with a range of different weather events.

6.4 ON-ISLAND DYNAMICS OF HOST AVAILABILITY

Large and stable patches of multiple host plants occur in PNG, likely promoting high rates of host plant occupancy on favourable host types. In stark contrast to PNG, host abundance and stability throughout the TS/NPA varies considerably in space and time. This could be partly because host plants are spatially fragmented in the TS/NPA due to ocean and land barriers, but potentially host plants are temporally fragmented as

well, due to location-specific cultivation practices. The high levels of host plant fragmentation appear to be responsible for patchy host plant occupation throughout the TS/NPA. For this reason, host plant availability is likely to be the most important determinant of *E. flavipes* establishment success, population growth and persistence in the Torres Strait.

6.5 POPULATION GENETICS AND CONNECTIVITY

In chapter five, information on hypothesised dispersal mechanisms was combined with analyses of population genetic structure to determine whether long-distance wind-assisted dispersal from PNG was primarily responsible for immigration into the TS/NPA. Analysis of data from eight microsatellites in 648 individuals suggest that frequent, wind-assisted immigration from multiple sources in PNG contributes significantly to repeated colonisation of Torres Strait islands close to PNG. In contrast, intermittent long-distance, wind assisted immigration better explains patterns of genetic diversity and structure in the southern Torres Strait and on the tip of mainland Australia. Significant genetic structuring associated with the presence of clusters of highly related individuals occurs throughout the region. In general, this suggests that following colonisation by small numbers of individuals, population growth on each island is kin-structured with little post-establishment movement. There is some evidence that secondary movements between islands are restricted by quarantine zones. Results of chapter five suggest that control of the planthopper may be very difficult on islands close to PNG given the propensity for annual invasion, but may be achievable further south where local populations appear highly independent and isolated.

6.6 MANAGEMENT RECOMMENDATIONS

Planthoppers are entirely dependent upon the presence of suitable host plants (Denno & Perfect 1994). Results of chapter four suggest that the availability of host plants in the TS/NPA can be severely impacted by local cultivation practices; yet long-term detection records indicate *E. flavipes* presence in the TS/NPA for at least 28 years.

Intensive sampling during this research revealed that within a two year period, *E. flavipes* populations appear to 'blink' in and out of existence, in that extinction and recolonisation events cause the distribution of populations to change in space and over time (Chapter four; Anderson *et al.* 2009). Individual populations may be transient because of variation in host plant availability but long-term regional persistence is ensured; results suggest this is because annual re-colonisation occurs via wind-assisted, long-distance immigration from PNG.

Allsopp (1991) suggested eradication of *E. flavipes* in the TS/NPA may be in order, but no further moves were made to enable this. Cultivation practices, such as tip-pruning, burning, and replanting of stalks could severely reduce infestation size (Chapter four). A planned, simultaneous tip-pruning effort throughout the region may effectively remove *E. flavipes* only host, thereby reducing and/ or eradicating infestations (Chapter four; Anderson *et al.* 2009). Despite this strategy, permanent eradication of *E. flavipes* would appear unlikely on islands close to PNG given the suggested high propensity for seasonal recolonisation. Certainly, a 'rain of propagules' enhances establishment and survival (Simberloff 2009), but annual tip-pruning may achieve a temporary reduction in population size. In contrast, a similar tip-pruning strategy may achieve permanent eradication in the southern TS given the apparent lower invasion pressures and isolation.

There is some evidence that suggests anthropogenic movement occurs, and is restricted by quarantine zone (Chapter 5). Such movement cannot be prevented, only discouraged through penalties. A tip-pruning strategy on the other hand may reduce the likelihood of an infested stalk being moved. Also, cultivation practices that are likely to impact on host availability and indirectly reduce infestation size could be encouraged, especially close to PNG. Finally, provision of sugarcane varieties resistant to Ramu stunt disease will reduce the likelihood of disease establishment. Pre-emptive management of *E. flavipes* is highly preferable over the eradication of Ramu stunt disease should it be detected in the TS/NPA.

By manipulating host availability, a reduction in the overall TS/NPA infestation and eradication on islands close to mainland Australia and on the NPA may actually be achievable. In this way, *E. flavipes* overall invasion success and persistence in the TS/NPA could be significantly reduced, and the creation of a planthopper-free buffer zone in the southern Torres Strait may reduce the current invasion threat to commercial

Australian sugarcane. *E. flavipes* management is highly preferable over Ramu stunt disease eradication should it be detected in the TS/NPA.

Controlling Ramu stunt disease, should it enter the TS/NPA, would prove much more difficult than control of *E. flavipes* in the manner suggested. The current cultivation practice of sharing sugarcane planting material may act to spread Ramu stunt, as the disease is systemic and known to spread via replanting of infected setts (Waller *et al.* 1987). Should disease control be required, entire plants would need to be removed, as opposed to the removal of just infested tops as for the control of *E. flavipes*. Culturally, the removal and destruction of only infested tops, even done repeatedly over time, is highly likely to be more acceptable to gardeners than the total removal of all sugarcane planting material, and the necessary provision of suitable replacement sugarcane. Therefore, the eradication of Ramu stunt disease would be infinitely more difficult than implementing a pre-emptive strategy aimed at managing or eradicating the disease vector *E. flavipes.*

Importantly, any control and/or eradication of *E. flavipes* populations in the manner recommended in this thesis be consultative before, during and after implementation, to gain co-operation and minimise impact in Aboriginal and Torres Strait islander communities.

6.7 FUTURE RESEARCH

Illegal movement of sugarcane is suspected to occur from coastal PNG villages into the Torres Strait. Data from chapter four showed the private allele count from two particular TS populations was incredibly high, indicating that those alleles did not occur anywhere else in the TS/NPA (see Appendix 1). Both populations were sampled in 2008, and were not present in 2006. One of these occurred on a sugarcane patch in the 'PNG garden' on Dauan Island. *E. flavipes* samples collected from PNG coastal villages during routine Australian Quarantine Inspection Service plant health surveys could be targeted for genetic analyses, and included in a population connectivity analysis with samples from throughout the TS/NPA, which have already been typed. Such analyses may provide evidence that illegal across-country movement occurs. Time constraints meant that this could not be done for inclusion in this thesis.

E. flavipes capability for wind-assisted immigration from PNG was not directly quantified in this study due to the expense and time involved. However, such studies have been undertaken in the Torres Strait before (Johansen *et al.* 2003), and would be worthwhile repeating for *E. flavipes*. Using results from the simulations conducted in chapter three, peak immigration times may be targeted for high-level air sampling, for which a number of methods are recommended, including using nets suspended under aircraft (Dingle 1996). Quantification of such movement would validate the simulation results and conclusions drawn in chapter three.

A larger-scale study looking at recolonisation following extinction would provide excellent insight into the invasion process in the Torres Strait. The three Top Western islands of Boigu, Saibai and Dauan could be targeted for total *E. flavipes* eradication via tip-pruning as suggested. Given the hypothesised propensity for large numbers of annual introductions at these islands, the time to recolonisation and numbers of founders could be studied. Alternatively, the occurrence of exotic fruit flies such on the Top Western islands during the summer monsoon could be used to similar advantage.

REFERENCES

Ahmed S, Compton SG, Butlin RK, Gilmartin PM (2009) Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proceedings of the National Academy of Sciences of the United States of America,* **106,** 20342-20347.

Allendorf FW, Lundquist LL (2003) Introduction: population biology, evolution, and control of invasive species. *Conservation Biology,* **17,** 24-30.

Allsopp PG (1991) Quarantine survey of sugarcane pests and diseases on the Torres Strait Islands 1989. *Proceedings of Australian Society of Sugar Cane Technologists,* **13,** 83-87.

Alvarez N, Hossaert-McKey M, Restoux G, Delgado-Salinas A, Benrey B (2007) Anthropogenic effects on population genetics of phytophagous insects associated with domesticated plants. *Evolution,* **61,** 2986-2996.

Amalraj VA, Balasundaram N (2006) On the taxonomy of the members of '*Saccharum* complex'. *Genetic Resources and Crop Evolution,* **53,** 35-41.

Anderson KL, Deveson TE, Sallam N, Congdon BC (2010) Wind-assisted migration potential of the island sugarcane planthopper *Eumetopina flavipes* (Hemiptera: Delphacidae): implications for managing incursions across an Australian quarantine frontline. *Journal of Applied Ecology,* **47,** 1310–1319.

Anderson KL, Sallam M, Congdon BC (2007) Long distance dispersal by *Eumetopina flavipes* (Hemiptera: Delphacidae), vector of Ramu stunt: is culture contributing? *Proceedings of Australian Society of Sugar Cane Technologists,* **29,** 226-234.

Anderson KL, Sallam N, Congdon BC (2009) The effect of host structure on the distribution and abundance of the island sugarcane planthopper, *Eumetopina flavipes* Muir, vector of Ramu stunt disease of sugarcane. *Virus Research,* **141,** 247-257.

Andrewartha HG, Birch LC (1954) *The distribution and abundance of animals,* Chicago, The University of Chicago Press.

Ashley MV, Berger-Wolk TY, Caballero IC, Chaovalitwongse W, DasGupta B, Sheikh SI (2009) Full sibling reconstruction in wild populations from microsatellite

genetic markers. *Computational Biology: New Research* (eds Russe AS), pp. 231-258. Nova Publishers, Hauppauge, N.Y.

Austerlitz F, JungMuller B, Godelle B, Gouyon PH (1997) Evolution of coalescence times, genetic diversity and structure during colonization. *Theoretical Population Biology,* **51,** 148-164.

Australian Government (1908) *Quarantine Act No. 3 (Incorporating Act No. 158 of 2007),* Canberra, Office of Legislative Drafting and Publishing, Attorney-General's Department.

Australian Government Department of Foreign Affairs and Trade (1985) *Treaty between Australia and the independent State of Papua New Guinea concerning sovereignty and maritime boundaries in the area between the two Countries, including the area known as Torres Strait, and related matters,* Canberra, Australian Government Publishing Service.

Babbage R (1990) *The strategic significance of Torres Strait,* Canberra, The Australian National University.

Balloux F, Lugon-Moulin N (2002) The estimation of population differentiation with microsatellite markers. *Molecular Ecology*, **11,** 155-165.

Barham AJ (2000) Late Holocene maritime societies in the Torres Strait Islands, northern Australia - cultural arrival or cultural emergence? *East of Wallace's Line: Studies of past and present maritime cultures of the Indo-Pacific region* (eds O'Connor S & Veth P), pp. 223-314. A. A. Balkema, Rotterdam.

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal Royal Statistical Society: Series B,* **57,** 289-300.

Blackburn F (1984) *Sugar-cane,* New York, Longman Group Limited.

Bohonak AJ, Davies N, Villablanca FX, Roderick GK (2001) Invasion genetics of New World medflies: testing alternative colonisation scenarios. *Biological Invasions,* **3,** 103-111.

Bourke MR (1990) Subsistence food production systems in Papua New Guinea: old changes and new changes. *Pacific production systems: approaches to economic prehistory - papers from a Symposium at the XV Pacific Science Congress, Dunedin, New Zealand 1983* (eds Yen DE & Mummery JMJ). The Australian National University, Canberra.

Braithwaite KS, Croft BC, Magarey RC (2007) Progress in identifying the cause of Ramu stunt disease of sugarcane. *Proceedings of Australian Society of Sugar Cane Technologists,* **29,** 235-241.

Brandes EW (1956) Origin, dispersal and use in breeding of the Melanesian garden sugarcane and their derivatives, *Saccharum officinarum* L. *Proceedings of International Society of Sugar Cane Technologists,* **9,** 709-780.

Brower LP (1985) New perspectives on the migration biology of the monarch butterfly, *Danaus plexippus* L. *Migration: Mechanisms and Adaptive Significance* (eds Rankin MA), pp. 748-785. Marine Science Institute, Port Aransas, Texas.

Cantrell BK, Chadwick B, Cahill A (2002) *Fruit fly fighters - eradication of the papaya fruit fly,* Collingwood, CSIRO Publishing.

Carlton JT, Ruiz GM (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. *Invasive alien species: a new synthesis* (eds Mooney HA, Mack R, McNeely JA, Neville LE, Schei PJ & Waage JK), pp. 36-58. Island Press, Washington.

Carter M (2001) New evidence for the earliest human occupation in Torres Strait, northeastern Australia. *Australian Archaeology,* **52,** 50 - 52.

Chapman JW, Reynolds DR, Mouritsen H, Hill JK, Riley JR, Sivell D, Smith AD, Woiwod IP (2008) Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology,* **18,** 514-518.

Claridge MF, Vrijer PWF (1994) Reproductive behaviour: the role of acoustic signals. *Planthoppers: their ecology and management* (eds Denno RF & Perfect JT), pp. 216-233. Chapman & Hall, New York.

Clayton WD, Renvoize SA (1999) *Genera Graminum: grasses of the world,* Kew, Royal Botanic Gardens.

Colautti RI, Manca M, Viljanen M, Ketelaars HAM, Burgi H, Macisaac HJ, Heath DD (2005) Invasion genetics of the eurasian spiny waterflea: evidence for bottlenecks and gene flow using microsatellites. *Molecular Ecology,* **14,** 1869-1879.

Congdon BC, Piatt JF, Martin K, Friesen VL (2000) Mechanisms of population differentiation in marbled murrelets: historical versus contemporary processes. *Evolution,* **54,** 974-986.

Croft BJ, Braithwaite KS (2006) Management of an incursion of sugarcane smut in Australia. *Australasian Plant Pathology,* **35,** 113-122.

Cronin JT (2009) Movement, colonization, and establishment success of a planthopper of prairie potholes, *Delphacodes scolochloa* (Hemiptera: Delphacidae). *Ecological Entomology,* **34,** 114-124.

Crow JF, Kimura M (1970) *An introduction to population genetics theory,* New York, Harper and Row.

Debach P (1965) Some biological and ecological phenomena associated with colonising entomophagous insects. *The genetics of colonising species* (eds Baker HG & Stebbins GL), pp. 287-306. Academic Press, New York.

Denno RE, Cheng JY, Roderick GK, Perfect JT (1994) Density-related effects on the components of fitness and population dynamics of planthoppers. *Planthoppers: their ecology and management* (eds Denno RE & Perfect JT), pp. 257-281. Chapman and Hall, New York.

Denno RF (1993) Life history strategies of immigrant planthoppers. *Evolution of insect pests: patterns of variation* (eds Kim KC & McPheron BA), pp. 183-201. John Wiley & Sons Inc, New York.

Denno RF (1994a) Influence of habitat structure on the abundance and diversity of planthoppers. *Planthoppers: their ecology and management* (eds Denno RF & Perfect JT), pp. 140-159. Chapman and Hall Inc., New York.

Denno RF (1994b) Life history variation in planthoppers. *Planthoppers: their ecology and management* (eds Denno RF & Perfect J, T.), pp. 163-215. Chapman and Hall Inc., New York.

Denno RF, McClure MS (Eds.) (1983) *Variable plants and herbivores in natural and managed systems,* London, Academic Press.

Denno RF, Peterson MA, Weaver M, R. , Hawthorne DJ (2008) Life history evolution in native and introduced populations. *Evolutionary biology of plant and insect relationships* (eds Tilmon KJ). University of California Press, Berkeley, CA, USA.

Denno RF, Roderick GK (1990) Population biology of planthoppers. *Annual Review of Entomology,* **35,** 489-520.

Denno RF, Roderick GK, Olmstead KL, Dobel HG (1991) Density-Related Migration in Planthoppers (Homoptera, Delphacidae) - the Role of Habitat Persistence. *American Naturalist,* **138,** 1513-1541.

Deveson ED, Drake AV, Hunter DM, Walker PW, Wang HK (2005) Evidence from traditional and new technologies for northward migrations of Australian plague

locusts (*Chortoicetes terminifera*) (Walker) (Orthoptera: Acrididae) to western Queensland. *Austral Ecology,* **30,** 920-935.

Dingle H (1996) *Migration: The biology of life on the move,* Oxford, Oxford University Press.

Drake JM, Lodge DM (2006) Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. *Biological Invasions,* **8,** 365-375.

Eastwood D (1990) Ramu stunt disease - development and consequences at Ramu Sugar Ltd. *Sugar Cane,* **2,** 15-19.

Excoffier L, Foll M, Petit RJ (2009) Genetic consequences of range expansions. *Annual Review of Ecology Evolution and Systematics,* **40,** 481-501.

Excoffier LG, Laval G, Schneider S (2005) Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online,* **1,** 47-50.

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics,* **164,** 1567-1587.

Farrow RA, Drake AV (1978) *Report on insect migration studies in the Torres Strait (1977 - 1978),* Canberra, CSIRO. Division of Entomology.

Farrow RA, Ritchie SA, Johansen CA, Morrisen A (2001) *Report to Australian Quarantine and Inspection Service: an investigation of insect migration in the northern Torres Strait between southern Papua and Saibai Island with special reference to mosquito vectors of Japanese encephalitis,* Canberra, Tilembeya Consulting.

Floerl O, Inglis GJ (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biological Invasions,* **7,** 589-606.

Foll M, Gaggiotti O (2006) Identifying the environmental factors that determine the genetic structure of populations. *Genetics,* **174,** 875-891.

Foster M (2010) Sugar. *Australian Commodities,* **17** 310-316.

Gaggiotti O, Foll M (2010) Quantifying population structure using the F-model. *Molecular Ecology Resources,* **10,** 821-830.

Gaggiotti OE, Bekkevold D, Jorgensen HBH, Foll M, Carvalho GR, Andre C, Ruzzante DE (2009) Disentangling the effects of evolutionary, demographic and

environmental factors influencing genetic structure of natural populations: Atlantic herring as a case study *Evolution*, **63,** 2939-2951.

Glaubitz JC (2004) CONVERT: a user friendly program to reformat diploid genotypic data for commonly used population genetic software packages. *Molecular Ecology Notes*, **4,** 309-310.

Google Inc. (2009) Google Earth Version v 5.1.3533.1731 *Available http://earth.google.com/ 25 May 2010*.

Grassl CO (1946) *Saccharum robustum* and other wild relatives of 'Noble' sugar canes. *Journal of the Arnold Arboretum*, **27,** 234-252.

Gregg PC, Del Socorro AP, Rochester WA (2001) Field test of a model of migration of moths (Lepidoptera : Noctuidae) in inland Australia. *Australian Journal of Entomology*, **40,** 249-256.

Grevstad F, S. (1999) Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biological Invasions*, **1,** 313-323.

Grilli MP (2006) Effect of local land use on populations of a disease vector planthopper. *Population Ecology*, **35,** 1254-1263.

Haddon AC (1908) *Reports of the Cambridge anthropological expedition to Torres Straits: Volume VI Sociology, magic and religion of the eastern Islanders*, London, Cambridge University Press.

Haddon AC (1912) *Reports of the Cambridge anthropological expedition to Torres Straits: Volume IV Arts and crafts*, London, Cambridge University Press.

Ham G, McGuire P, Kingston G (2000) Irrigation of sugarcane. *Manual of canegrowing* (eds Hogarth DM & Allsopp PG), pp. 369-377. Bureau of Sugar Experiment Stations, Brisbane.

Hanski I (1994) Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution*, **9,** 131-135.

Hanski I, Gilpin ME (1997) *Metapopulation biology: ecology, genetics and evolution*, San Diego, Academic Press.

Harris DR (1977) Subsistence strategies across Torres Strait. *Sunda and Sahul: prehistoric studies in southeast Asia, Melanesia and Australia* (eds Allen J, Golson J & Jones P), pp. 421–464. Academic Press, London.

Hedrick P, Gilpin M (1997) Genetic effective size of a metapopulation. *Metapopulation biology: ecology, genetics and evolution* (eds Hanski I & Gilpin ME), pp. 165-181. Academic Press, San Diego.

Hodkinson TR, Chase MW, Lledo MD, Salamin N, Renvoize SA (2002) Phylogenetics of *Miscanthus, Saccharum* and related genera (Saccharinae, Andropogoneae, Poaceae) based on DNA sequences from ITS nuclear ribosomal DNA and plastid trnL intron and trnL-F intergenic spacers. *Journal of Plant Research,* **115,** 381-392.

Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology,* **43,** 835-847.

Ingvarsson PK, Giles BE (1999) Kin-structured colonization and small-scale genetic differentiation in *Silene dioica*. *Evolution,* **53,** 605-611.

Irvine JE (1999) *Saccharum* species as horticultural classes. *Theoretical and Applied Genetics,* **98,** 186-194.

Johansen CA, Farrow RA, Morrisen A, Foley P, Bellis GA, Van Den Hurk AF, Montgomery B, Mackenzie JS, Ritchie SA (2003) Collection of wind-borne haematophagous insects in the Torres Strait, Australia. *Medical and Veterinary Entomology,* **17,** 102-109.

Johnson CJ, Gillingham MP (2008) Sensitivity of species-distribution models to error, bias, and model design: an application to resource selection functions for woodland caribou. *Ecological Modelling,* **213,** 143-155.

Johnson MS (1988) Founder effects and geographic variation in the land snail *Theba pisana*. *Heredity,* **61,** 133-142.

Jones OR, Wang JL (2010) COLONY: a program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources,* **10,** 551-555.

Kalinowski S, Taper M, Marshall T (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology,* **16,** 1099-1106.

Kalinowski ST (2005) HP-Rare: A computer program for performing rarefaction on measures of allelic diversity *Molecular Ecology Notes,* **5,** 187-189.

Kellogg EA (1998) Relationships of cereal crops and other grasses. *Proceedings of the National Academy of Sciences of the United States of America,* **95,** 2005-2010.

Kikkawa J, Monteith G, Ingram G (1981) Cape York Peninsula: major region of faunal interchange. *Ecological biogeography of Australia* (eds Keast A), pp. 1697-1742. Dr W. Junk, The Hague.

Kisimoto R (1976) Synoptic weather conditions inducing long-distance immigration of planthoppers, *Sogatella furcifera* Horvath and *Nilaparvata lugens* Stal. *Ecological Entomology,* **1,** 95-109.

Kisimoto R, Rosenberg JL (1994) Long-distance migration in delphacid planthoppers. *Planthoppers: their ecology and management* (eds Denno RF & Perfect JT), pp. 302-322. Chapman and Hall New York.

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution,* **16,** 199-204.

Komonen A, Grapputo A, Kaitala V, Kotiaho JS, Paivinen J (2004) The role of niche breadth, resource availability and range position on the life history of butterflies. *Oikos,* **105,** 41-54.

Krebs C, J. (2001) *Ecology: the experimental analysis of distribution and abundance,* California, Benjamin Cummings.

Kuniata LS, Chandler KJ, Nagaraja H, Young GR (2006) Phytophagous insects on broadacre sugarcane in Papua New Guinea. *PNG Journal of Agriculture, Forestry and Fisheries,* **49,** 31-35.

Kuniata LS, Young GR, Pais E, Jones P, Nagaraja H (1994) Preliminary observations on *Eumetopina* sp. (Hemiptera: Delphacidae) as a vector of Ramu stunt disease of sugarcane in Papua New Guinea. *Journal of the Australian Entomological Society,* **33,** 185-186.

Kuno E (1979) Ecology of the brown planthopper in temperate regions *Brown planthopper: threat to rice production in Asia* (eds International Rice Research Institute), pp. 45-60. International Rice Research Institute Manila, Phillipines.

Lawrence D (1994) Customary exchange across Torres Strait. *Memoirs of the Queensland Museum,* **34,** 241-446.

Lawton JH, Brown KC (1986) The population and community ecology of invading insects. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* **314,** 607-617.

Lawton JH, Schroder D (1977) Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature,* **265,** 137-140.

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society B: Biological Science,* **269,** 2407-3413.

Lindsay D (1987) *Report on aerial littoral surveillance and Northern Australian Quarantine Strategy: interim report by the Quarantine Review Committee,* Canberra, Australian Government Publishing Services.

Lintermans M (2004) Human-assisted dispersal of alien freshwater fish in Australia. *New Zealand Journal of Marine and Freshwater Research,* **38,** 481-501.

Lockwood JL, Hoopes M, Marchetti M (2007) *Invasion ecology,* Oxford, Blackwell Publishing.

Lubina JA, Levin SA (1988) The spread of a reinvading species - range expansion in the California sea otter. *American Naturalist,* **131,** 526-543.

MacArthur R, Wilson EO (1967) *The theory of island biogeography,* Princeton, Princeton University Press.

Mack RN, Lonsdale WM (2001) Humans as global plant dispersers: getting more than we bargained for. *Bioscience,* **51,** 95-102.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications,* **10,** 689-710.

Magarey RC, Suma S, Irawan, Kuniata LS, Allsopp PG (2002) Sik na binatang bilong suka - diseases and pests encountered during a survey of *Saccharum* germplasm 'in the wild' in Papua New Guinea. *Proceedings of Australian Society of Sugar Cane Technologists,* **24,** 219-227.

May YY (1975) Study of two forms of the adult *Stenocranus minutus*. *Transactions of the Royal Entomological Society of London,* **127,** 241-254.

McClure MS (1983) Competition between herbivores and increased resource heterogeneity. *Variable plants and herbivores in natural and managed systems* (eds Denno RF & McClure MS), pp. 125-153. Academic Press, New York.

Moore DR (1978) *Islanders and aborigines at Cape York,* Melbourne, The Dominion Press.

Ohkubo N (1973) Experimental studies on the flight of planthoppers by the tethered flight technique. I. Characteristics of flight of the brown planthopper *Nilaparvata lugens* (Stal) and effects of some physical factors. *Japan Journal of Applied Entomology Zoology,* **17,** 10-18.

Okubo A, Levin SA (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology,* **70,** 329-338.

Padgham DE, Perfect JT, Cook AG (1987) Flight behaviour in the brown planthopper, *Nilaparvata lugens* (Stal) (Homoptera: Delphacidae). *Insect Science and its Application,* **8,** 71-75.

Paijmans K (1976) *New Guinea vegetation,* Canberra, Australian National University Press.

Park SDE (2001) Trypanotolerance in west African cattle and the population genetic effects of selection. PhD Thesis. Dublin, University of Dublin.

Peakall R, Smouse P (2006) Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes,* **6,** 288-295.

Pemberton CE (1949) Notes on the life history of the sugar cane leaf hopper. *Hawaiian Planters' Record,* **53,** 205 - 210.

Perfect JT, Cook AG (1994) Rice planthopper population dynamics: a comparison between temperate and tropical regions. *Planthoppers: their ecology and management* (eds Denno RF & Perfect JT), pp. 282-301. Chapman and Hall, Inc., New York.

Peterson MA, Denno RF (1998) The influence of dispersal and diet breadth on patterns of genetic isolation by distance in phytophagous insects. *American Naturalist,* **152,** 428-446.

Petit RJ, El Mousadik A, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. *Conservation Biology,* **12,** 844-855.

Pheloung P (2003) An Australian perspective on the management of pathways for invasive species. *Invasive species: vectors and management strategies* (eds Ruiz GM & Carlton JT), pp. 249-269. Island Press, Washington.

Pilot M, Dahlheim ME, Hoelzel AR (2010) Social cohesion among kin, gene flow without dispersal and the evolution of population genetic structure in the killer whale (*Orcinus orca*). *Journal of Evolutionary Biology,* **23,** 20-31.

Pimentel D, Lach L, Zuniga R, Morrison D (1999) *Environmental and Economic Costs Associated with Non-indigenous Species in the United States,* Ithaca, New York, College of Agriculture and Life Sciences, Cornell University.

Plant Health Australia (2004) *National sugar industry biosecurity pPlan,* Canberra, National Plant Health Australia.

Puri K, Dietachmayer G, Mills GA, Davidson NE, Bowen RA, Logan LW (1998) The new BMRC limited area prediction system, LAPS. *Australian Meteorological Magazine,* **47,** 203-223.

Puth LM, Post DM (2005) Studying invasion: have we missed the boat? *Ecology Letters,* **8,** 715-721.

Queensland Environmental Protection Agency (2005) *Queensland Herbarium HERBRECS Database,* Brisbane, The State of Queensland.

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution,* 258-275.

Quinn G, Keough M (2006) *Experimental design and data analysis for biologists,* Cambridge, Cambridge University Press.

Regan HM, Colyvan M, Burgman MA (2002) A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications,* **12,** 618-628.

Reynolds DR, Riley JR, Armes NJ, Cooter RJ, Tucker MR, Colvin J (1997) Techniques for quantifying insect migration. *Methods in ecological and agricultural entomology* (eds Dent DR & Walton MP), pp. 111-145. CAB International, Wallingford, Oxon, UK.

Riley JR, Reynolds DR, Smith AD, Rosenberg LJ, Cheng XN, Zhang XX, Xu GM, Cheng JY, Bao AD, Zhai BP, Wang HK (1994) Observations on the autumn migration of *Nilaparvata lugens* (Homptera, Delphacidae) and other pests in East Central China *Bulletin of Entomological Research,* **84,** 389-402.

Ritchie SA, Rochester WA (2001) Wind-blown mosquitoes and introduction of Japanese Encephalitis into Australia. *Emerging Infectious Diseases,* **7,** 900-903.

Rochester WA, Dillon ML, Fitt GP, Zalucki MP (1996) A simulation model of the long-distance migration of *Helicoverpa* spp. moths. *Ecological Modelling,* **86,** 151-156.

Rollins LA, Woolnough AP, Sherwin WB (2006) Population genetic tools for pest management: a review. *Wildlife Research,* **33,** 251-261.

Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. *Trends in Ecology & Evolution,* **22,** 454-464.

Root RB (1973) Organisation of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). *Ecological Monographs,* **43,** 95-124.

Rosenberg LJ, Magor JI (1987) Predicting windborne displacements of the brown planthopper, *Nilaparvata lugens* from synoptic weather data. 1. Long-distance displacements in the north-east monsoon. *Journal of Animal Ecology*, **56,** 39-51.

Ruiz GM, Carlton JT (2003) *Invasive species: vectors and management strategies*, Washington, Island Press.

Sallam M, Anderson KL (2006) Preparation for invasion by the insect vector of Ramu Stunt. *BSES Bulletin*, **12,** 8-9.

Schowalter TD (2000) *Insect ecology: an ecosystem approach*, San Diego, Academic Press.

Seino H, Shiotsuki Y, Oya S, Hirai Y (1987) Prediction of long distance migration of rice planthoppers to northern Kyushu considering low-level jet stream. *Journal of Agricultural Meteorology*, **43,** 203-208.

Sherwin W, Moritz C (2000) Managing and monitoring genetic erosion. *Genetics, demography and viability of fragmented populations* (eds Young A & Clarke G). Cambridge University Press, Cambridge.

Simberloff D (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology Evolution and Systematics*, **40,** 81-102.

Slatkin M (2008) Linkage disequilibrium - understanding the evolutionary past and mapping the medical future. *Nature Reviews Genetics*, **9,** 477-485.

SPSS Inc. (2004) SPSS for Windows, Release 13.0.1. Chicago, SPSS Inc.

Stanaway MA, Zalucki MP, Gillespie PS, Rodriguez CM, Maynard GV (2001) Pest risk assessment of insects in sea cargo containers. *Australian Journal of Entomology*, **40,** 180-192.

Suppiah R (1992) The Australian summer monsoon - a review. *Progress in Physical Geography*, **16,** 283-318.

Technical Advisory Panel on exotic fruit flies for Plant Health Committee and Primary Industries Standing Committee (2004) *A long-term containment strategy for exotic fruit flies in Torres Strait*, Cairns, Australia, Department of Agriculture, Fisheries and Forestry Australia and Department of Employment, Economic Development and Innovation

Thomas C, Hanski I (1997) Butterfly metapopulations. *Metapopulation biology: ecology, genetics and evolution* (eds Hanski I & Gilpin ME), pp. 359–386. Academic Press, San Diego.

Thomas CD (1994) Extinction, colonization and metapopulations: environmental tracking by rare species. *Conservation Biology,* **8,** 373-378.

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London B: Biological Sciences,* **267,** 139-145.

Thomas CD (2001) Scale, dispersal and population structure. *Insect movement: mechanisms and consequences: Proceedings of the Royal Entomological Society's 20th Symposium* (eds Woiwod IP, Reynolds DR & Thomas CD), pp. 321-336. CABI Publishing, Wallingford.

Thresh JM, Scorer RS, Harrington R, Pedgley DE, Nuttall PA, Sellers RF (1983) The long-range dispersal of plant viruses by arthropod vectors *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* **302,** 497-528.

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes,* **4,** 535-538.

Verhoeven KJF, Simonsen KL, McIntyre LM (2005) Implementing false discovery rate control: increasing your power. *Oikos,* **108,** 643-647.

Walker D (1972) *Bridge and barrier: the natural and cultural history of Torres Strait,* Canberra, Australian National University.

Waller JM, Egan BT, Eastwood D (1987) Ramu stunt, an important new sugarcane disease in Papua New Guinea. *Tropical Pest Management,* **33,** 347-349.

Waloff N, MacFadyen A (1980) Studies on Grassland Leafhoppers (Auchenorrhyncha, Homoptera) and their Natural Enemies. *Advances in Ecological Research*, pp. 81-215. Academic Press.

Wasserman SS, Futuyma DJ (1981) Evolution of host plant utilization in laboratory populations of the southern cowpea weevil, *Callosobruchus maculatus* Fabricius (Coleoptera: Bruchidae). *Evolution,* **35,** 605-617.

Watanabe T, Seino H (1991) Correlation between the immigration area of rice planthoppers and the low-level jet stream in Japan. *Applied Entomology and Zoology,* **26,** 457-462.

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. *Evolution,* **38,** 1358-1370.

Williamson M (1996) *Biological invasions,* London, Chapman & Hall.

Williamson MH (1981) *Island populations,* Oxford, Oxford University Press.

Williamson MH, Fitter A (1996) The characters of successful invaders. *Biological Conservation,* **78,** 163-170.

Wilson SW, Mitter C, Denno RF, Wilson MR (1994) Evolutionary patterns of host plant use by delphacid planthoppers and their relatives. *Planthoppers: their ecology and management* (eds Denno RF & Perfect JT), pp. 7-113. Chapman & Hall, Inc, London.

With KA (2002) The landscape ecology of invasive spread. *Conservation Biology,* **16,** 1192-1203.

Worner SP (2002) Predicting the invasive potential of exotic insects. *Invasive arthropods in agriculture: problems and solutions* (eds Hallman G, J. & Schwalbe CP), pp. 119-137. Science Publishers Inc., New Hampshire.

APPENDIX 1. SUMMARY OF *E. FLAVIPES* GENETIC VARIATION AT 8 MICROSATELLITE LOCI

Part 1. Bamaga to Waiben. Summary of genetic variation for *Eumetopina flavipes* at 8 microsatellite loci for each population plus the overall data set, in the Torres Strait and on the northern peninsula area of Cape York, Queensland, Australia; number of alleles (N_A), expected heterozygosity (H_E), observed heterozygosity (H_O) (*) indicates significance at $P = 0.05$, allelic richness (A_R), private allelic richness (A_P), multilocus inbreeding coefficient (F_{IS}), mean population F_{ST} (F_{ST}), proportion significant linkage disequilibrium per population ($P > 0.05$) (% sig. LD).

Locus	Measure	Bamaga1	Bamaga2	Bamaga3	Bamaga4	New Mapoon1	New Mapoon2	Keriri1	Waiben1
	n	26	27	25	25	25	17	22	25
8TER 10	N_A	3	4	3	3	2	1	3	3
	H_E	0.544	0.610	0.56571	0.59673	0.08156	0	0.63848	0.28408
	H_O	0.539	0.815	0.56	0.6	0	0	1*	0.08*
1TER 327	N_A	4	4	5	2	4	3	3	2
	H_E	0.492	0.431	0.6977	0.37224	0.5913	0.12298	0.65041	0.50286
	H_O	0.154*	0.333*	0.33333*	0.4	0.73913	0.125	0.42857*	0.72
2TER 427	N_A	4	4	4	4	2	2	4	2
	H_E	0.571	0.684	0.72754	0.45633	0.5102	0.48663	0.75377	0.42857
	H_O	0.24*	0.667	0.47826*	0.48	0.52	0.41176	1*	0.36
3TER 527	N_A	4	5	5	5	2	1	5	3
	H_E	0.359	0.768	0.57551	0.69143	0.50286	0	0.76638	0.54776
	H_O	0.385	0.815	0.44	0.76	0.56	0	1*	0.76
4TER 627	N_A	1	4	1	4	2	2	3	1
	H_E	0	0.686	0	0.47918	0.45796	0.51337	0.65539	0
	H_O	0	0.815	0	0.44*	0.44	0.47059	0.81818	0
5TER 727	N_A	4	6	4	5	2	2	4	2
	H_E	0.55	0.837	0.45959	0.60408	0.50286	0.51515	0.72404	0.48082
	H_O	0.577	0.889	0.44	0.56	0.48	0.88235*	1*	0.36
7TER 1027	N_A	2	3	2	1	2	2	2	1
	H_E	0.238	0.238	0.07837	0	0.4898	0.37077	0.38372	0
	H_O	0.269	0.259	0.08	0	0.64	0.47059	0.5	0
Overall	N_A	22	30	24	24	16	13	24	14
	H_E	0.393	0.608	0.44349	0.45714	0.44808	0.28699	0.65317	0.32058
	H_O	0.309	0.656	0.333084	0.46286	0.48273	0.33718	0.82096	0.32571
	A_R	2.25	3.31	2.49	2.53	2	1.64	3.11	1.76
	A_P	0	0.06	0	0.01	0.06	0	0.59	0
	F_{IS}	0.251*	-0.0591	0.22417*	-0.00534	-0.11942	-0.2816	-0.32309	0.10588
	F_{ST}	0.549	0.409	0.511	0.517	0.66	0.716	0.518	0.72
	% sig. LD	0	0	0.047619	0	0	0	0.52381	0.14286

Part 2. Ngurupai to Mabuiag. Number of alleles (N_A), expected heterozygosity (H_E), observed heterozygosity (H_O) (*) indicates significance at P = 0.05, allelic richness (A_R), private allelic richness (A_P), multilocus inbreeding coefficient (F_{IS}), mean population F_{ST} (F_{ST}), proportion significant linkage disequilibrium per population ($P > 0.05$) (% sig. LD).

Locus	Measure	Ngurupai1	Ngurupai2	Ngurupai3	Masig1	Masig2	Masig3	Mabuiag1	Mabuiag2	Mabuiag3
	n	25	25	21	20	15	9	14	13	9
8TER 10	N_A	3	3	2	4	6	5	4	3	4
	H_E	0.46939	0.59673	0.39605	0.707	0.812	0.791	0.67989	0.62462	0.79085
	H_O	0.44**	0.56	0.52381	0.79	0.933	0.889	0.92857*	0.84615	1
1TER 327	N_A	3	3	3	6	5	5	5	2	3
	H_E	0.54531	0.63032	0.62253	0.82	0.81	0.745	0.69312	0.47077	0.68627
	H_O	0.4	0.79167	0.52381	1	1	0.444	0.57143	0.69231	0.11111*
2TER 427	N_A	2	2	2	4	3	6	3	2	3
	H_E	0.3942	0.50709	0.25087	0.74	0.645	0.8116	0.64815	0.49231	0.21569
	H_O	0.43478	0.66667	0.28571	0.9	1*	1	1*	0.76923	0.22222
3TER 527	N_A	5	6	10	4	4	8	6	4	3
	H_E	0.69681	0.69878	0.66899	0.76	0.722	0.924	0.80423	0.77899	0.66013
	H_O	0.70833	0.8	0.71429	1*	0.857	1	1*	1*	1
4TER 627	N_A	2	2	9	4	3	4	4	2	2
	H_E	0.15603	0.11968	0.55981	0.74	0.595	0.399	0.64286	0.52	0.52941
	H_O	0.08333	0.125	0.42857*	0.94*	0.5	0.444	0.71429	1*	1*
5TER 727	N_A	1	2	2	4	4	5	6	3	4
	H_E	0	0.08156	0.39605	0.7	0.738	0.667	0.79365	0.64923	0.73333
	H_O	0	0.08333	0.42857	0.8	0.929*	0.444	1*	1*	1
7TER 1027	N_A	1	3	1	4	4	4	4	4	1
	H_E	0	0.22204	0	0.68	0.59	0.712	0.67989	0.75385	0
	H_O	0	0.24	0	1*	0.643	0.778	1**	1	0
Overall	N_A	17	21	29	30	29	37	32	20	20
	H_E	0.32310	0.40803	0.41347	0.74	0.702	0.721	0.70597	0.61282	0.51653
	H_O	0.29521	0.46667	0.41497	0.92	0.83741	0.714	0.88776	0.9011	0.61905
	A_R	1.95	2.26	2.43	3.75	3.58	4.16	3.55	2.76	2.63
	A_P	0.01	0.01	0.37	0.32	0.23	0.46	0.34	0.03	0.37
	F_{IS}	0.08148	-0.1788	-0.05941	-0.29	-0.3363	0.048	-0.30207	-0.46725	0.02141
	F_{ST}	0.651	0.561	0.429	0.37	0.34	0.198	0.313	0.511	0.48
	% sig. LD	0	0.28571	0.09524	0.619	0.90476	0.048	0.61905	0.571429	0.04762

Part 3. Badu to Dauan. Number of alleles (N_A), expected heterozygosity (H_E), observed heterozygosity (H_O) (*) indicates significance at $P = 0.05$, allelic richness (A_R), private allelic richness (A_P), multilocus inbreeding coefficient (F_{IS}), mean population F_{ST} (F_{ST}), proportion significant linkage disequilibrium per population ($P > 0.05$) (% sig. LD).

Locus	Measure	Badu1	Badu2	Badu3	Dauan1	Dauan2	Dauan3
	n	25	13	25	25	16	25
8TER 10	N_A	3	2	5	11	9	9
	H_E	0.50694	0.27077	0.64539	0.77306	0.7908	0.82319
	H_O	0.52	0.15385	0.66667	0.92	0.73333*	0.82609
1TER 327	N_A	5	5	4	9	6	9
	H_E	0.7551	0.71429	0.56245	0.82535	0.58462	0.81905
	H_O	0.8	0.90909	0.4	0.58333*	0.30769*	0.38889*
2TER 427	N_A	3	4	5	6	6	7
	H_E	0.50857	0.51515	0.68889	0.62057	0.8004	0.67592
	H_O	0.56	0.45455	0.73913	0.58333	0.9375	0.72
3TER 527	N_A	5	5	7	13	10	10
	H_E	0.73714	0.80519	0.68816	0.86879	0.87356	0.86892
	H_O	0.8	0.72727	0.40909*	0.91667	0.93333*	0.95455
4TER 627	N_A	3	3	4	6	9	6
	H_E	0.65878	0.671	0.59091	0.75918	0.81855	0.7611
	H_O	0.72	0.63636	0.63636	0.76	0.6875*	0.77273
5TER 727	N_A	4	4	5	9	9	8
	H_E	0.64898	0.72105	0.68883	0.7649	0.81609	0.76216
	H_O	0.64	0.6	0.75	0.56*	0.46667*	0.81818
7TER 1027	N_A	2	2	3	5	4	6
	H_E	0.18367	0.07692	0.27343	0.74939	0.70115	0.58188
	H_O	0.2	0.07692	0.30435	0.68*	1*	0.57143
Overall	N_A	25	25	33	59	53	55
	H_E	0.57131	0.53920	0.59115	0.76589	0.76931	0.75603
	H_O	0.60571	0.50829	0.55794	0.71476	0.72372	0.72169
	A_R	2.89	2.97	3.13	4.53	4.5	4.47
	A_P	0	0	0.36	0.2	0.44	0.29
	F_{IS}	-0.04582	-0.12941	-0.0455	0.09538	-0.0137	-0.0622
	F_{ST}	0.446	0.39	0.368	0.126	0.134	0.146
	% sig. LD	0.142857	0.04762	0.14286	0.66667	0.57143	0.52381

Part 4. Saibai to Boigu. Number of alleles (N_A), expected heterozygosity (H_E), observed heterozygosity (H_O) (*) indicates significance at $P = 0.05$, allelic richness (A_R), private allelic richness (A_P), multilocus inbreeding coefficient (F_{IS}), mean population F_{ST} (F_{ST}), proportion significant linkage disequilibrium per population ($P > 0.05$) (% sig. LD).

Locus	Measure	Saibai1	Saibai2	Saibai3	Saibai4	Boigu1	Boigu2	Boigu3	Boigu4
	n	25	25	25	25	25	25	11	15
8TER 10	N_A	6	9	7	8	10	9	6	6
	H_E	0.74204	0.82041	0.76522	0.82029	0.86122	0.77796	0.72632	0.74769
	H_O	0.68	0.8	0.73913	0.6087	0.88	0.76	0.6	0.46154
1TER 327	N_A	5	8	9	7	8	9	5	6
	H_E	0.68213	0.79344	0.81878	0.8227	0.78901	0.78964	0.64502	0.79894
	H_O	0.78261	0.79167	0.6	0.66667	0.66667	0.59091	0.27273*	0.57143
2TER 427	N_A	4	5	5	5	6	6	5	6
	H_E	0.65714	0.70776	0.72898	0.72125	0.71099	0.70449	0.77124	0.75132
	H_O	0.52	0.72	0.72	0.61905	0.54167	0.72	0.77778	0.71429
3TER 527	N_A	7	10	10	9	13	14	6	9
	H_E	0.70204	0.85633	0.76507	0.86152	0.8746	0.88019	0.75817	0.88308
	H_O	0.68	0.76	0.83333	0.68182	0.94444	0.73913**	0.55556	0.61538
4TER 627	N_A	4	5	6	3	5	6	4	4
	H_E	0.68898	0.57796	0.7151	0.63508	0.64058	0.74645	0.69697	0.65833
	H_O	0.68	0.56	0.76	0.8125	0.43478	0.83333	0.66667	0.75
5TER 727	N_A	6	10	7	8	13	9	6	3
	H_E	0.71691	0.85878	0.8484	0.82051	0.86531	0.8049	0.82632	0.30115
	H_O	0.69565	0.88	0.83333	0.8	0.76	0.52**	0.4**	0.33333
7TER 1027	N_A	4	3	4	5	7	7	5	5
	H_E	0.22449	0.40163	0.36571	0.50887	0.67347	0.79755	0.68346	0.64368
	H_O	0.24	0.36	0.4	0.5	0.64	0.88	0.8	0.6
Overall	N_A	36	50	48	45	62	60	37	39
	H_E	0.63053	0.71661	0.71532	0.74146	0.77360	0.78588	0.72900	0.68346
	H_O	0.61118	0.69595	0.69797	0.66982	0.69537	0.72048	0.58182	0.578
	A_R	3.4	4.25	4.08	4.21	4.6	4.56	4.03	4.01
	A_P	0.15	0.1	0.09	0.22	0.17	0.22	0.31	0.25
	F_{IS}	0.00208	-0.00024	0.04311	0.03756	0.09195	0.08129	0.15535	0.11481
	F_{ST}	0.312	0.175	0.181	0.182	0.099	0.141	0.198	0.207
	% sig. LD	0.14286	0.095238	0	0	0.14286	0.38095	0.14286	0.19048