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RECOVERY OF THE FRESHWATER LENTIC INSECT FAUNA IN THAILAND FOLLOWING THE TSUNAMI OF 2004

Robert W. Sites
Enns Entomology Museum, Division of Plant Sciences, University of Missouri, Columbia, Missouri 65211, USA
Email: sitesr@missouri.edu

Akekawat Vitheepradit
Enns Entomology Museum, Division of Plant Sciences, University of Missouri, Columbia, Missouri 65211, USA
Email: akekawat@gmail.com

ABSTRACT. – The tsunami of 26 December 2004 inundated the coastlines of many Southeast Asian countries, including Thailand. The force of the surge was devastating to the extent that hundreds of thousands of humans were killed, whereas the effect on non-human biota, including insects, remains largely unreported. Along the Andaman Sea coastline of Thailand, we sampled lentic (pond) habitats within the area directly affected by the tsunami and other reference ponds slightly inland to determine the rate and trajectory of community recovery following extirpation. Our first samples were taken five months after the tsunami, which marked the end of a dry season. By that time, many impacted ponds already had substantial freshwater recharge through rainfall, and conductivity had fallen to approximately 10% that of seawater. An insect community with a mean richness of 20 taxa was present already, whereas the unaffected inland ponds had a mean richness of 27 taxa. Insect tolerance to salinity in general appears to be greater and taxonomically more widespread than previously considered. Three additional sampling periods were spaced over the next 12 months. Two-way ANOVA tests for species richness among higher taxa revealed significant differences among sampling periods for total Insecta and four orders separately (Odonata, Hemiptera, Coleoptera, and Diptera), and six subordinate taxa (Anisoptera, Zygoptera, Gerridae, Notonectidae, Dytiscidae, and Chironomidae). Patterns of species richness in impacted ponds across sampling periods were evaluated with Discriminant Function Analysis separately using ordinal and family richness values. Using ordinal richness values, 55.0% of the ponds were classified to the correct sampling period, whereas when using family richness values, 92.5% of the ponds were classified correctly. A parsimony analysis was performed to evaluate community succession and recovery trajectory. Numerous tangential trajectories are evident, suggesting that the communities of the impacted ponds are not assembling toward the taxonomic composition of the unaffected ponds, but to one or more alternative stable states. Taxonomic composition was evaluated also by clustering Jaccard's Similarity scores. On each of the four sampling dates and overall, fidelity of pond type based on the taxonomic composition is distinct, suggesting that the community in the impacted ponds has not demonstrated any signs of shifting toward that of the unaffected ponds. In addition to the evaluation of inundated and unaffected pond communities, a series of peat swamps that had been collected in 1994 and 1995 were resampled to obtain comparable post-tsunami data. We found only 16 of the 33 taxa previously recorded and substantially fewer individuals.

KEY WORDS. – tsunami, lentic, aquatic insect, community recovery, alternative stable state.

INTRODUCTION

The Indian Ocean tsunami of 26 December 2004 affected the coastlines of at least twelve Southeast Asian countries as well as the Indian subcontinent, eastern Africa and countless islands and atolls. Its effect on humanity was profound, resulting in over 300,000 dead or missing (Tsokos et al., 2006). Afterward, much attention was understandably focused on the human side of the tragedy, with relatively little effort directed toward understanding the tsunami's effect on other aspects of the biota, including insects. Recognizing this investigative shortcoming, Krishnankutty (2006) called for future studies on tsunami-disturbance changes in ten areas, including studies on species richness and community structure of the macro and meio fauna.

Shortly after the tsunami, a rapid assessment of environmental damage was conducted (UNEP, 2005). The countries suffering the most extensive damage to coastal ecosystems were Indonesia, Sri Lanka, India, Maldives, and Thailand

(Shaw, 2008). Of the few published studies addressing the effect on the non-human biota, marine invertebrates have been most favored, and were generally shown to suffer only short term, minor setbacks. For example, infection rates and diversity of trematode cercariae were not significantly different after the tsunami, although three host snail species had disappeared (Harada et al., 2007); littorinid mollusks were unaffected by the tsunami (Sanpanich et al., 2006); coral damage at the Similan Islands ranged from 7 to 39% (Cavanich et al., 2008) and Brown (2005) predicted complete recovery in 10 years; urchins and brittle stars were disturbed only temporarily and had returned to shallow basins and intertidal areas by 2007 (Kendall et al., 2009); and the meiofauna recolonized the beaches quickly and was considered to be highly resilient to this disturbance (Grzelak et al., 2009).

Plant communities have been the subject of several studies relating to the effects of the tsunami. In two studies conducted in Thailand, 11 of 13 species of seaweed at Talibong Island were strongly affected by the tsunami (Prathep et al., 2008); however, submergent sea grass beds at Laem Mae Heng were largely undamaged (Kendall et al., 2009). Most reports of the effect on mangroves indicate that the seaward side suffered substantial damage (Kendall et al., 2009), but most of the mangrove forests did not sustain serious damage, and in fact, only 0.2% of the mangrove area in Thailand suffered any damage (UNEP, 2005). In part because mangroves have evolved to adapt to changing shoreline conditions and disturbance events, they are considered to be resilient and offer some coastal protection by absorbing a portion of the energy of a tsunami (Alongi, 2008).

Several insect studies focusing on Diptera were undertaken following the tsunami. Assessment of muscoid fly populations was conducted in southern India (Srinivasan et al., 2006, 2009); malaria risk in Sri Lanka was shown to be unchanged by the tsunami (Briët et al., 2005, 2006); and the distribution and response to saline conditions of chironomid larvae associated with the tsunami impacted ponds of Thailand were presented by Cranston (2007).

Small lentic water bodies (i.e. ponds) are scattered along the Andaman Sea coastline of Thailand. Ponds of this type generally harbor a diverse community of aquatic insects adapted for freshwater conditions. Although some aquatic insects have tolerance to brackish conditions, the replacement of freshwater with seawater in these basins during the tsunami clearly rendered them uninhabitable for this insect community. How quickly the lentic insect community recovered, and toward what taxonomic composition was the focus of this investigation. Thus, presented here is the response of the entire lentic insect fauna of ponds of the western coastal floodplain of Thailand to the tsunami of 26 December 2004. Included are assessments of the recovery of various taxa at different taxonomic levels, and a consideration of the trajectory of community recovery. Further, a published pre-tsunami survey of aquatic hexapods in a series of peat swamps was repeated and results are presented.

MATERIALS AND METHODS

Two quantitative investigations were conducted during this study. First, a quantitative assessment of the recovery of the lentic insect community in the inundated ponds was conducted. Second, a series of peat swamps on Phuket Island that had been sampled in 1994 and 1995 (Watanasit, 1995) was resampled using identical collection techniques to those of Watanasit to provide a direct pre-and post-tsunami comparison of the fauna. In addition, mangroves and intertidal areas were qualitatively sampled to determine the presence of the Gerromorpha that typically inhabit these areas.

Recovery of Inundated Ponds

Thirty-three sites (Fig. 1, Table 1) in the provinces of Ranong, Phang Nga, Phuket, Krabi, Trang, and Satun along the Andaman Sea coastline of Thailand were selected for sampling four times over a 13 month period, beginning five months after the tsunami of 26 December, 2004. These included 12 ponds directly inundated by the tsunami with replacement by seawater, and 10 unaffected (non-inundated) ponds located within 1 km inland of the incursion of seawater. Of these, two inundated and one unaffected ponds were disqualified because these inundated ponds continued to maintain extremely high conductivity levels, suggesting periodic influx of seawater during high tides, and the unaffected pond had become dry because of agricultural activity. Thus, 19 ponds were retained for statistical analyses. The tsunami occurred at the end of the 2004 wet season. The sampling dates were chosen to coincide with climatologically and biologically meaningful points in time as follows: 22 May to 5 June 2005, end of first dry season; 2–11 August

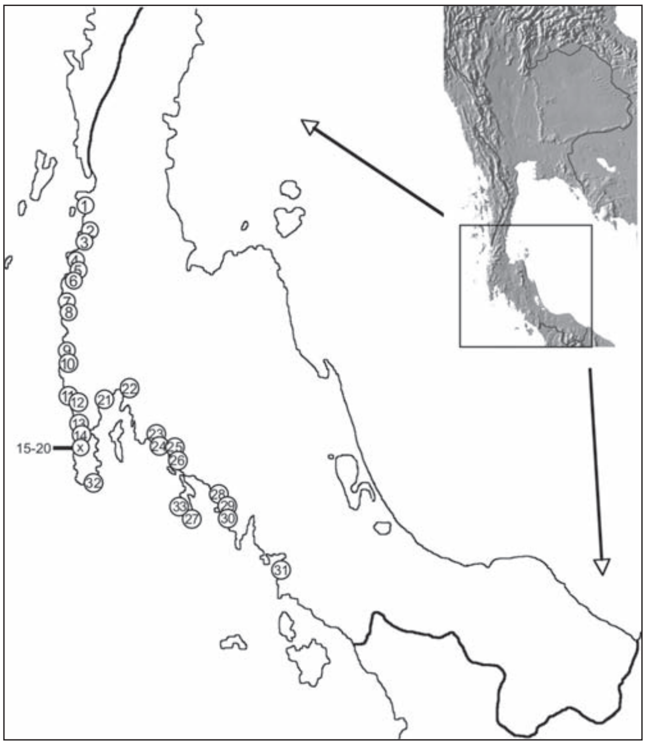

Fig. 1. Map of the Isthmus of Kra showing all collection sites. Site numbers correspond with data in Table 1.

Table 1. Collection localities for 33 sites sampled following the tsunami of 26 December 2004. Each locality was assigned a specific site number. Associated L-numbers (one/sampling period) are unique site/date identifiers and can be used to reference photographs via the Locality Image Database of the Enns Entomology Museum web site.

Site	**L-numbers**	**Locality Data**	**Type**
1	836, 874, 921b	Ranong Province, Biosphere Reserve, Mangrove Research Center, 9°52.488'N 98° 36.245'E	mangrove
2	788, 837, 875, 922	Ranong Province, Laem Son National Park, pond near Headquarters, 9°36.247'N 98° 28.005'E	inundated
3	789, 838, 876, 923	Ranong Province, Laem Son National Park, pond in front of officer house, 9°36.118'N 98°28.074'E	inundated
4	791, 839, 877	Ranong Province, Suk Samran; Pra Pas Beach, 9°22.479'N 98°23.893'E	inundated[a]
5	794, 840	Ranong Province, Suk Samran; Tumbon Kam Puan, 9°20.397'N 98°24.772'E	unaffected[a]
6	793, 841, 878, 924	Phang Nga Province, Amphur Khura Buri; Ao Keuy Beach, 9°18.005'N 98°22.798'E	inundated
7	818, 843, 880, 927	Phang Nga Province, Amphur Takua Pa, Tumbon Bang Nai Si; Ban Bang Yai, 8°25.950'N 98°23.192'E	unaffected
8	819, 844, 881, 928	Phang Nga Province, Amphur Takua Pa, Tumbon Koag Kien, Ban Bang Klag Klang, 8°52.469'N 98°22.679'E	unaffected
9	820, 845, 882, 929	Phang Nga Province, Amphur Takua Pa, Tumbon Bang Muang, Ban Nam Khem, 8°51.391'N 98°15.989'E	inundated
10	823, 846, 883, 930	Phang Nga Province, Amphur Takua Pa, Nang Tong Beach, 8°38.906'N 98°14.833'E	inundated
11	824, 847, 884, 932	Phang Nga Province, Khao Lampi-Hat Thai, Mueang National Park, 8°28.312'N 98°13.672'E	inundated
12	825, 849, 886, 935	Phang Nga Province, Amphur Thai Mueang, Tumbon Na Teoy; Ban Bang Klee, 8°18.655'N 98°17.552'E	unaffected
13	817, 853, 890, 937	Phuket Province, Amphur Takua Thung, Tumbon Krasom; Ban Bang Mak, 8°11.087'N 98°17.350'E	inundated[a]
14	816, 852, 889, 936	Phuket Province, Amphur Thalang, Tumbon Mai Khao; Moo Ha, 8°10.718'N 98°17.611'E	unaffected
15	808, 856, 892, 941	Phuket Province, Amphur Thalang; Jae Son, 8°9.532'N 98°17.756'E	peat swamp
16	809, 855, 897, 942	Phuket Province, Amphur Thalang; Jig, 8°8.772'N 98°17.892'E	peat swamp
17	807, 859, 896, 940	Phuket Province, Amphur Thalang; Laem Yot, 8°8.325'N 98°17.927'E	peat swamp
18	810, 857, 895, 943	Phuket Province, Amphur Thalang; Jud, 8°7.930'N 98°18.156'E	peat swamp
19	815, 858, 894, 939	Phuket Province, Amphur Thalang; Mai Khao, 8°7.461'N 98°18.193'E	peat swamp
20	811, 854, 893, 938	Phuket Province, Amphur Thalang; Thung Tien, 8°7.258'N 98°18.165'E	peat swamp
21	826, 850, 888, 945	Phang Nga Province, Amphur Takua Thung, Tumbon Krasom ; Ban Bang Mak, 8°24.553'N 98°27.434'E	unaffected
22	827, 851, 887, 946	Phuket Province, Amphur Mueang; Tumbon Na Pring, 8°31.750'N 98°32.001'E	unaffected
23	805, 863, 902, 948	Krabi Province, Amphur Mueang, Noppharat Thara Beach, 8°2.625'N 98°48.517'E	inundated
24	806, 862, 901, 947	Krabi Province, Amphur Mueang, Klong Maung Beach, 8°2.979'N 98°45.540'E	inundated
25	828, 864, 904, 951	Krabi Province, Amphur Nuea Khlong, Tumbon Nuea Khlong, Ban Paga Sai, 8°2.619'N 99°1.144'E	unaffected
26	829, 867, 903, 952	Krabi Province, Amphur Nuea Khlong, Tumbon Klong Kanan, Ban Klong Kanan, 8°1.045'N 99°0.450'E	unaffected
27	804, 865, 905, 949	Krabi Province, Amphur Ko Lanta; Klong Dao Beach, 7°38.662'N 99°1.395'E	inundated
28	831, 868, 908, 955	Trang Province, Amphur Sikao; Tumbon Mai Fard, Ban Klong Maeng, 7° 30.170'N 99°20.541'E	unaffected
29	830, 869, 907, 954	Trang Province, Amphur Sikao; Chao Mai Beach, 7°26.842'N 99°20.647'E	inundated
30	832, 870, 906, 953	Trang Province, Amphur Sikao; ca. 8 km N, Chao Mai National Park, 7°28.155'N 99°20.158'E	mangrove
31	833, 871, 909, 956	Satun Province, Amphur Thung Wa; Tumbon, Khon Klan; near Klong Rawi, 7°0.472'N 99°40.754'E	mangrove
32	860, 861, 891, 944	Phuket Province, Phuket Marine Biological, Research Center, 7°48.096'N 98°24.468'E	intertidal
33	866, 950	Krabi Province, Amphur Ko Lanta; Klong Dao Beach, 7°38'N 99°1'E	intertidal

[a] Site that was disqualified from inclusion in statistical analyses (see text).

2005, short decline in precipitation during wet season; 3–10 January 2006, end of wet season; 7–14 June 2006, end of second dry season. Thus, our first samples were taken following one dry season. Conductivity of the water in each pond was measured on each sampling date using an Oakton CON 11 conductivity and TDS meter. These data also served as an indirect measure of osmolarity. Photographs of all sites (identified as L-numbers) in which these samples were taken are available in a Locality Image Database via a link from the internet site of the Enns Entomology Museum, University of Missouri.

Qualitative samples were taken with D-nets and were sorted in the field with a sufficiently rigorous protocol to enable the comparison of community similarity between pond types in space and over time. More specifically, samples were taken by sweeping an aquatic D-net over the substrate and water surface, and when present, also through algae and rooted macrophytes of each pond. Net contents were sorted in white pans and insect specimens were placed into containers with 80% ethyl alcohol. Alcohol was changed within 48 hr to compensate for dilution. Stop rules were employed such that sampling continued at a site until each of two collection teams found no recognizably new morphospecies in two consecutive samples. Aerial adult insects were also collected when observed to assist with identifications of taxa with aquatic immature stages. A presence/absence matrix was created in Excel, version 11.3.7 (Microsoft Corp., Redmond, WA) from which statistical analyses were performed using SPSS statistical software (SPSS Inc., Chicago, IL).

Differences in species richness between pond types and over time were examined from both univariate and multivariate perspectives. Two-way analyses of variance with repeated measures were performed on log-transformed richness data between inundated and unaffected ponds among the four sampling periods. Separate analyses were performed on total Insecta; the orders Ephemeroptera, Odonata, Hemiptera, Coleoptera, and Diptera; and for families with at least five species. Mauchly's Test of Sphericity was performed to test for equality in the variance of differences. For analyses in which the assumption of sphericity was violated, the Huynh-Feldt epsilon correction (Huynh & Feldt, 1976) was applied.

Patterns of species richness within only the inundated ponds were examined by computing species richness values for each of a number of taxa to be used as independent variables with discriminant function analysis (DFA). As such, richness values for five orders and 27 families were used in separate analyses to search for distinctions among the four sampling periods for inundated ponds. Pairwise F-tests associated with DFA determined which sampling periods significantly differed from each of the other sampling periods. The subsequent classification phase of DFA then assigned each pond to a sampling period based on the linear combination of variables from each discriminant function axis.

Percent of correct assignments may be used as a separate measure of the singularity in the suite of species richness values of a sampling period.

Parsimony analysis has been suggested to be an appropriate technique by which to examine the successional trajectory of communities following catastrophic events resulting in defaunation (Wenzel & Luque, 2008), and the coastal lentic community following the tsunami seems perfectly suited for this analysis. Prior to performing parsimony analysis, all unaffected ponds within each of the four sampling periods were pooled such that a single community with all taxa for each sampling period was established to represent the maximum taxon community on that sampling date. These communities were used because we do not have pre-tsunami community data from inundated ponds, and our best estimate of end-state conditions is represented by the community in the nearby unaffected ponds. In addition, a hypothetical zero community was created, thereby generating a gradient from zero taxa to the maximum taxa communities along which the impacted pond communities can organize. Thus, a data matrix including presence or absence of taxa for all 10 impacted ponds over 4 sampling periods, as well as the hypothetical zero and 4 pooled unaffected ponds was created and analyzed using PAUP, version 4.0b10 (Swofford, 2003). A heuristic search was conducted in PAUP, generating a strict consensus tree, which was modified graphically for presentation using Mesquite, version 1.06 (Maddison & Maddison, 2005).

Similarities in taxonomic composition were quantified using Jaccard's index (Sneath & Sokal, 1973; Magurran, 2004) based on a presence-absence matrix for the insect fauna of each pond. More specifically, similarity ($\mathbf{S_{ij}}$) between any pair of ponds **i** and **j** is given by

$$\mathbf{S_{ij} = a/(a + b + c)}$$

where **a** is the number of taxa shared in common, **b** in the number of taxa in pond **i** but not pond **j**, and **c** is the number of taxa in pond **j** but not pond **i**. Joint absences (taxa that do not occur in either pond **i** or **j**) of taxa found at other ponds in the study are not considered in these calculations of similarity. The relationship among ponds in taxonomic composition as estimated by Jaccard's index was clustered, using an unweighted paired group means algorithm (UPGMA). The resulting cluster dendrograms grouped all ponds based on taxonomic composition.

Discriminant Function, Jaccard's similarity, and cluster analyses were performed using SPSS, version 4.0 (SPSS Inc, Chicago, IL), and the two-way ANOVA was performed using SPSS version 16.0 (SPSS Inc, Chicago, IL).

Peat Swamp Survey

A survey of the aquatic hexapods in six peat swamps of Phuket Island, conducted in 1994 and 1995 (Watanasit, 1995), included samples taken during both wet season and dry seasons. These peat swamps are adjacent to the airport on Phuket Island and were under seawater during the tsunami. Watanasit's procedures called for one sample per peat swamp by sweeping an aquarium net (13 x 13 cm) with mesh size 250 µ through aquatic plants for 5 minutes (Watanasit, 1995;

pers. comm). We repeated the field procedures of Watanasit to obtain directly comparable post-tsunami data.

RESULTS

All totalled, 212 taxa of insects were collected, of which 199 (Table 2) were entered into the database for use in analyses of inundated and unaffected ponds. Although many larvae were identified to species, the Culicidae were collapsed to generic recognition for analyses because many specimens suffered sufficient damage that precluded specific identification. The insects subjected to analysis represented only the orders Odonata, Ephemeroptera, Hemiptera, Coleoptera, and Diptera. Odonata (both Zygoptera and Anisoptera) were prolific and diverse, however, our state of taxonomic knowledge of the immature stages in Southeast Asia is quite poor, therefore these larvae were assigned morphospecies identities. Odonata larvae are an ontogenetic moving target because critical diagnostic attributes can change dramatically as they develop, thus some very early instars were discounted from the analysis since they could not be associated reliably with later instars. Adult odonates were sampled around the perimeter of the ponds and 24 taxa were identified (Table 3). However, whether or not these adult taxa developed in the associated ponds is not known, although one species [*Tramea limbata* (Desjardins): Libellulidae] was successfully reared from a pond-collected immature and this species was represented in the adult collections.

At least two undescribed species of Hemiptera were discovered during this project, including of the genera *Ranatra* (Nepidae) and *Paraplea* (Pleidae). Additional undescribed species of Coleoptera and Diptera are probable. The mangroves and intertidal areas yielded aquatic Hemiptera in the first sampling period that were not found in the ponds or peat swamps, including two species of *Asclepios* and three species of *Halobates* (Gerridae), two species of *Xenobates* and one species of *Halovelia* (Veliidae), and one species of *Hermatobates* (Hermatobatidae) (Table 2).

We measured the conductivity of Indian Ocean seawater at 41,900 µS, and as expected, conductivity for the inundated ponds was higher than that of unaffected ponds, but progressively declined over time (Fig. 2). Although other related variables (e.g., salinity, total dissolved solids) should be considered when examining cause and effect relationships, elevated levels of conductivity undoubtedly played a role in shaping community recovery and succession as dilution occurred following the tsunami.

Differences in Species Richness

Two-way ANOVA tests for species richness (Table 4) of higher taxa revealed significant differences among sampling periods for total Insecta, each order separately (except Ephemeroptera), and six subordinate taxa (Anisoptera, Zygoptera, Gerridae, Notonectidae, Dytiscidae, and Chironomidae) (Table 4). The richness difference for Culicidae approached significance (p=0.054). In contrast, only Ephemeroptera and Nepidae exhibited significant differences in richness between impacted and unaffected ponds. Overall insect species richness steadily increased through the first two sampling periods and peaked during the third sampling period (January 2006) (Fig. 3). An overall reduction in richness occurred in the fourth sampling period (May 2006).

Patterns of species richness in impacted ponds across sampling periods were evaluated with DFA separately using ordinal and family richness values, and contours around scatterplot distribution limits are graphically presented (Fig. 4). The analysis using ordinal richness values as independent variables required two functions to account for 98.0% of the variation among pond communities. Hemiptera and Coleoptera were most important components in the first function, and Odonata and Ephemeroptera in the second function (Table 5, Fig. 4a). Three of the six pairwise contrasts revealed significantly different communities: period 1 differed from 3 and 4, and 2 differed from 3. In the subsequent classification phase, 55.0% of the ponds correctly classified to their actual sampling period.

The analysis using family richness values as independent variables required three functions to account for 100% of the variation among pond communities. Ceratopogonidae and various families of Hemiptera and Coleoptera were the most important variables in the first function (Table 6, Fig. 4b). Four of the six pairwise contrasts revealed significantly different communities. Only period 4 was not significantly different from 2 or 3. In the subsequent classification phase, 92.5% of the ponds were classified correctly to their actual sampling period.

Taxonomic Composition

We performed parsimony analysis using species in each inundated pond to evaluate community succession and recovery toward hypothetical end-state conditions,

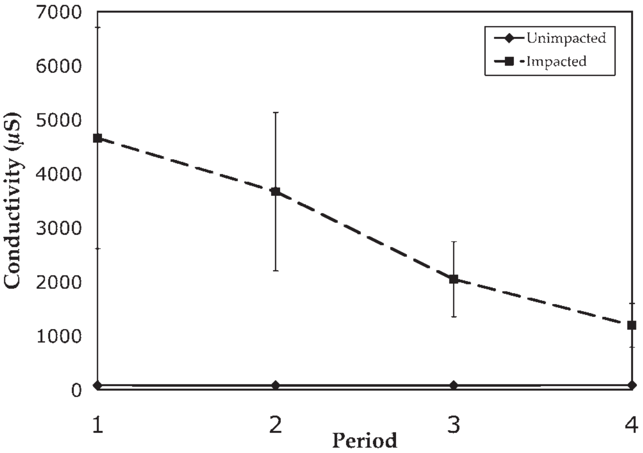

Fig. 2. Mean levels of conductivity (µS) in tsunami-inundated and unaffected ponds from which insect communities were sampled from May 2005 to June 2006.

Table 2. Taxa collected in ponds inundated by the tsunami, comparable ponds slightly inland, impacted peat swamps, and other water bodies impacted by the tsunami of 2004.

Taxon	Inundated	Unaffected	Peat	Other[a=]
EPHEMEROPTERA				
Baetidae				
Cloeon sp.	X	X	X	
Caenidae				
Caenis sp.	X	X	X	
ODONATA				
Zygoptera				
Lestidae	X	X		
Calopterygidae A	X	X		
Calopterygidae B	X	X		
Coenagrionidae A	X	X	X	
Coenagrionidae B	X	X	X	
Coenagrionidae C	X	X	X	
Coenagrionidae D	X	X	X	
Coenagrionidae E	X	X		
Coenagrionidae F	X	X		
Coenagrionidae G	X	X		
Coenagrionidae H	X	X		
Coenagrionidae I	X			
Protoneuridae			X	
Anisoptera				
Aeshnidae A	X	X		
Aeshnidae B	X	X		
Corduliidae A	X	X		
Corduliidae B	X	X		
Libellulidae				
Tramea limbata (Desjardins)	X	X		
Libellulidae A	X	X		
Libellulidae B	X	X		
Libellulidae C	X	X		
Libellulidae D	X	X		
Libellulidae E	X	X		
Libellulidae F	X	X		
Libellulidae G	X	X		
Libellulidae H	X	X		
Libellulidae I	X	X		
Libellulidae J	X	X		
Libellulidae K	X	X		
Libellulidae L	X	X		
Libellulidae M	X	X		
Libellulidae N	X	X		
Libellulidae O	X	X		
Libellulidae P	X	X		
Libellulidae Q	X			
Libellulidae R	X			
Libellulidae S	X			
Macromiidae A	X	X	X	
Macromiidae B	X			
Gomphidae				
? *Gomphidia* or *Ictinogomphus*	X	X		
HEMIPTERA				
Belostomatidae				
Diplonychus rusticus (Fab.)	X	X	X	
Lethocerus indicus Lepeletier & Serville	X	X		
Nepidae				
Cercotmetus brevipes Montandon	X	X	X	
Laccotrephes sp. A			X	
Laccotrephes sp. B		X		
Ranatra longipes thai Lansbury	X	X	X	
Ranatra varipes Stål	X	X	X	
Ranatra sp.		X		

Table 2. Cont'd.

Taxon	Inundated	Unaffected	Peat	Other[a=]
Micronectidae				
Micronecta fugitans Breddin		X		
Micronecta grisea (Fieber)	X	X	X	
Micronecta haliploides Horvath		X		
Micronecta ludibunda langkawa Wrobleski		X	X	
Micronecta punctata (Fieber)	X	X	X	
Micronecta quadristrigata Breddin	X		X	
Micronecta scutellaris (Stål)	X	X	X	
Micronecta sp. A	X		X	
Micronecta sp. B	X	X	X	
Micronecta sp. C	X	X		
Micronecta sp. D	X	X		
Micronecta sp. E	X			
Micronecta sp. F			X	
Micronecta sp. G			X	
Naucoridae				
Naucoris scutellaris Stål	X	X		
Ctenipocoris asiaticus Amyot & Serville	X	X	X	
Helotrephidae				
Tiphotrephes sp.		X		
Pleidae				
Paraplea frontalis (Fieber)	X	X	X	
Paraplea liturata (Fieber)	X	X	X	
Paraplea sp.	X	X		
Notonectidae				
Anisops sp. A	X	X		
Anisops sp. B	X	X	X	M
Anisops sp. C	X	X	X	
Anisops sp. D	X	X		
Aphelonecta gavini Lansbury	X	X	X	
Nychia sappho Kirkaldy	X	X	X	
Gerridae				
Aquarius adelaidis (Dohrn)			X	
Asclepios annandalei Distant				M
Asclepios sp.				M
Limnogonus f. *fossarum* (Fabricius)	X	X	X	M
Limnogonus hungerfordi Andersen		X	X	
Limnogonus nitidus (Mayr)	X	X	X	M
Limnogonus pectoralis (Mayr)	X			M
Limnometra ciliata Mayr	X	X		
Neogerris assimilis Andersen	X	X	X	
Neogerris parvulus (Stål)		X	X	
Rhagadotarsus kraepelini Breddin	X	X	X	
Halobates flaviventris Eschscholtz				I
Halobates hayanus White				I
Halobates proavus White				I
Mesoveliidae				
Mesovelia horvathi Lundblad	X	X	X	
Mesovelia vittigera Horvath	X	X	X	
Hebridae				
Hebrus sp. A	X	X	X	
Hebrus sp. B		X		
Veliidae				
Microvelia sp. A	X	X	X	
Microvelia sp. B	X	X	X	
Microvelia sp. C	X	X	X	
Neoalardus typicus (Distant)		X		
Xenobates argentatus Andersen				M
Xenobates sp.				M
Halovelia malaya Esaki				I
Hydrometridae				
Hydrometra annamana Hungerford & Evans	X	X	X	
Hydrometra carinata Polhemus & Polhemus		X	X	

Table 2. Cont'd.

Taxon	Inundated	Unaffected	Peat	Other[a=]
Hydrometra chaweewanae Sites & Polhemus		X	X	
Hydrometra greeni Kirkaldy	X	X	X	
Hydrometra maidli Hungerford & Evans	X	X		
Hydrometra orientalis Lundblad	X	X	X	
Hermatobatidae				
Hermatobates singaporensis Cheng				I
COLEOPTERA				
Dytiscidae				
Copelatus sp. A	X	X	X	
Copelatus sp. B	X			
Cybister dehaanii Aube'		X	X	
Cybister rugosus (MacLeay)	X			
Cybister sugillatus Erichson	X		X	
Laccophilus uniformis Motschulsky	X	X	X	
Laccophilus parvulus obtusus Sharp	X	X	X	
Hyphydrus lyratus Swartz	X	X	X	
Hydaticus luzonicus Aube'	X	X	X	
Hydaticus fabricii MacLeay	X	X	X	
Laccophilus siamensis group		X	X	
Hydrovatus sp.	X	X	X	
Hydroglyphus orientalis Clark	X	X	X	
Leiodytes sp.	X	X	X	
Hydroglyphus sp.	X	X	X	
Rhantaticus congestus Klug	X	X	X	
Hydaticus bipunctatus Wehncke	X	X		
Eretes griseus Fabricius	X			
Hydaticus pacificus group	X			
Neptosternus riedeli Hendrich & Balke		X		
Noteridae				
Canthydrus sp. A		X	X	
Canthydrus sp. B	X	X	X	
Neohydrocoptus sp. A	X	X		
Neohydrocoptus sp. B		X		
Gyrinidae				
Dineutus spinosus Fabricius		X		M
Dineutus sp.		X		
Orectocheilus sp.	X	X	X	
Haliplidae				
Haliplus philippinus Chapin	X	X		
Haliplus pulchellus Clark	X	X		
Peltodytes sumatrensis Regimbart		X		
Scirtidae				
Unknown A	X	X	X	
Hydrophilidae				
Agraphydrus sp.		X	X	
Allocotocerus muelleri		X		
Amphiops sp.	X	X	X	
Berosus (*Enoplorus*) sp.	X		X	
Berosus (s.str.) *pulchellus* MacLeay	X	X	X	
Chaetarthria sp.	X			
Chasmogenus abnormalis Sharp		X		
Coelostoma sp.	X	X	X	
Enochrus (*Methydrus*) *esuriens* (Walker)	X	X	X	
Enochrus (*Methydrus*) *nigropiceus* (Mots.)	X	X		
Enochrus tetraspilus (Regimbart)	X	X	X	
Helochares (*Hydrobaticus*) sp. A	X	X	X	
Helochares (*Hydrobaticus*) sp. B	X	X	X	
Helochares (s.str.) *taprobanicus* Sharp	X	X		
Hydrobiomorpha sp.	X	X		
Hydrochus sp.		X	X	
Paracymus sp.	X	X	X	
Regimbartia attenuata Fabricius	X	X	X	
Sternolophus sp.	X	X	X	

Table 2. Cont'd.

Taxon	Inundated	Unaffected	Peat	Other[a=]
Hydraenidae				
Hydraena sp.	X	X		
Limnebius sp.		X		
DIPTERA				
Chironomidae				
Ablabesmyia sp. A	X			
Ablabesmyia sp. B			X	
Chironomus sp. A	X	X	X	
Chironomus sp. B		X		
Clinotanypus sp.	X	X		
Conochironomus sp.	X	X		
Dicrotendipes pelechloris	X			
Dicrotendipes septemmaculatus (Becker)	X	X		
Dicrotendipes sarinae Epler	X			
Fittkauimyia sp.		X		
Kiefferulus calligaster (Kieffer)	X	X	X	
Kiefferulus barbatitarsis (Kieffer)	X	X	X	
Kiefferulus longilobus Kieffer	X		X	
Larsia sp.	X	X		
Parachironomus sp. A		X		
Parachironomus sp. B	X			
Parakiefferiela sp.		X		
Paramerina sp.	X	X		
Polypedilum sp.	X	X	X	
Polypedilum cfr *prasiogaster*		X		
Polypedilum leei type	X	X	X	I
Polypedilum nubifer (Skuse)		X		
Polypedilum nr *oresitrophus*	X			
Tanypod sp. A	X	X	X	
Tanypod (new Pentaneurini)	X			
Tanypus sp.		X	X	
Tanytarsus sp. A		X	X	
Tanytarsus sp. B	X	X	X	
Tanytarsus sp. C	X	X		
Zavreliella sp.		X		
Culicidae				
Anopheles (*Anopheles*) *barbirostris* van der Wulp	X			
Anopheles (*Anopheles*) *umbrosus* (Theobald)	X		X	
Anopheles (*Cellia*) *epiroticus* (Linton & Harbach)	X	X	X	
Anopheles (*Cellia*) *philippinensis* Ludlow		X		
Culex (*Culex*) *pseudovishnui* Colless	X	X	X	
Culex (*Culex*) *sitiens* Wiedemann	X			
Culex (*Culex*) *tritaeniorhynchus* Giles	X	X		
Culex (*Culex*) *vishnui* Theobald	X		X	
Culex (*Oculeomyia*) *bitaeniorhynchus* Giles		X		
Mansonia sp.		X		
Mimomyia (*Mimomyia*) *aurea* Leicester	X	X		
Mimomyia (*Mimomyia*) *chamberlaini* Ludlow		X		
Verrallina sp.	X			
Ceratopogonidae				
Culicoides sp.		X	X	
Palpomyiini prob. *Bezzia*	X	X		
Sphaeromiini	X	X	X	
Tabanidae				
Unknown A	X	X	X	
Stratiomyidae				
Unknown A	X	X	X	

[a] I, intertidal zone; M, mangrove.

Table 3. Adult Odonata collected from the perimeter of tsunami-inundated and nearby unaffected ponds.

- ODONATA
  - Coenagrionidae
    - *Agriocnemis* sp.
    - *Ceriagrion indochinense* Asahina
    - *Ischnura senegalensis* (Rambur)
    - *Pseudagrion australiasae* Selys
    - *Pseudagrion microcephalum* (Rambur)
  - Platycnemididae
    - *Copera ciliata* (Selys)
    - *Copera marginipes* (Rambur)
  - Protoneuridae
    - *Prodasineura* sp.
  - Libellulidae
    - *Acisoma panorpoides* Rambur
    - *Aethriamanta brevipennis* (Rambur)
    - *Brachydiplax chalybea* Brauer
    - *Brachydiplax farinosa* Krüger
    - *Crocothemis servilia* (Drury)
    - *Diplacodes trivialis* (Rambur)
    - *Indothemis* sp.
    - *Neurothemis fluctuans* (F.)
    - *Neurothemis fulvia* (Drury)
    - *Pantala flavescens* (F.)
    - *Orthetrum sabina* (Drury)
    - *Rhyothemis phyllis* (Sulzer)
    - *Rhyothemis triangularis* Kirby
    - *Tramea limbata* (Desjardins)
    - *Trithemis aurora* (Burmeister)
  - Aeshnidae
    - unidentified

represented by the community in nearby unaffected ponds. Two most parsimonious trees were produced, each with a treelength of 605 steps using 149 taxa to organize the succession of 45 ponds (including the zero taxa root and four control ponds). From these two trees, a consensus tree was created (Fig. 5) with a consistency index of 0.24 and retention index of 0.47. A main successional pathway to the control pond communities and five or more divergent trajectories are evident.

Comparison of taxonomic composition among inundated and unaffected ponds was accomplished also by clustering Jaccard's similarity scores separately for each sampling period. The resulting cluster dendrograms (Fig. 6) revealed faunas with high fidelity within pond type (inundated vs unaffected ponds). The few unaffected ponds whose taxonomic composition resulted in clustering with inundated ponds generally were those with higher apparent human disturbance. Otherwise, the dendrograms reflected very high consistency in linkage with like pond type. In a dendrogram comparing taxonomic composition among time periods, pooled ponds consistently exhibited greater similarity within pond type. Thus, overall composition remained more similar within inundated ponds and within unaffected ponds, than between pond types within sampling periods.

Peat Swamp Survey – Thirty-three taxa of aquatic hexapods were recorded by Watanasit (1995) among 6 peat swamps surveyed in the wet and dry seasons of 1994–95. After repeating his procedures in the wet and dry seasons of 2005 and dry season of 2006, we found substantially fewer taxa and individuals (Table 7). In fact, only 17 of the taxa recorded by Watanasit were recovered in our samples.

Voucher specimens of all taxa have been deposited in one or more of the following museum collections: Kasetsart University, Department of Entomology, Bangkok, Thailand; Enns Entomology Museum, University of Missouri, U.S.A.; institutional collections of the collaborating systematic specialists (see Acknowledgments).

DISCUSSION

With rare exception, every body of freshwater that is capable of sustaining an insect community does so. How the community assembles after a habitat becomes available has been and continues to be fertile ground for ecological debate. We observed rapid colonization despite high conductivity levels, and the tsunami impacted ponds maintained a different taxonomic composition from that of the unaffected ponds, although richness levels were not appreciably different.

As the seawater became diluted and insects recolonized the unoccupied ponds, we suggest that assembly of the community was controlled by a variety of factors that sequentially came to bear. Because taxa have differing dispersal abilities and search strategies, vagility and search efficiency were early limitations to recolonization. Strong, frequent fliers (e.g., Odonata) would find the ponds more quickly than weak, occasional fliers (e.g., Ephemeroptera). Once an insect located and entered the pond, physiological constraints related to osmolarity (and conductivity) precluded some taxa from becoming established. As dilution progressed, the conductivity immigration filter progressively became less of a barrier for an increasing number of insect taxa. For the insects that were able to tolerate the physiological challenge of high conductivity, biotic interactions became the next

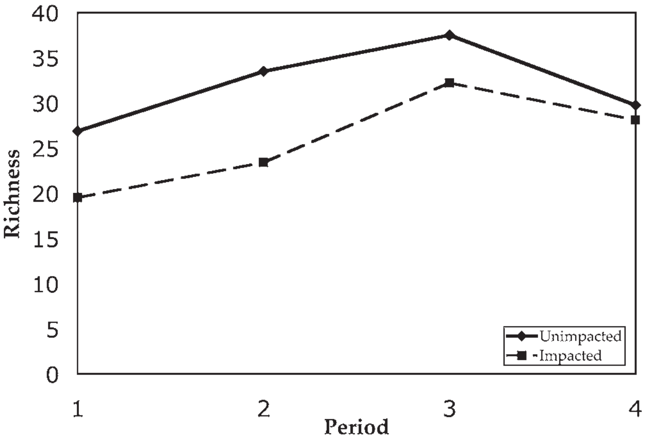

Fig. 3. Insect species richness levels over four time periods of tsunami-inundated and unaffected ponds within 1 km of the incursion of seawater.

Table 4. Two-Way ANOVA with repeated measures for differences in species richness[a] between pond type and among time periods (families with ≥ 5 species).

Higher Taxa

	Insecta		**Ephemeroptera**		**Odonata**		**Hemiptera**		**Coleoptera**		**Diptera**	
Factor	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***
Sampling Period	9.500	**0.000**	2.196	0.100	3.817	0.**015**	7.322	**0.000**	3.626	**0.019**	6.498	**0.001**
Pond Type	3.044	0.099	8.678	**0.009**	3.264	0.089	1.683	0.212	0.724	0.407	0.300	0.591
Interaction	0.805	0.497	1.021	0.391	0.682	0.567	3.066	**0.036**	0.532	0.646	1.135	0.344

Odonata Suborders

	Zygoptera		**Anisoptera**	
Factor	**F**	***p***	**F**	***p***
Sampling Period	3.034	**0.037**	3.100	0.**035**
Pond Type	4.238	0.055	1.304	0.269
Interaction	0.519	0.579	0.478	0.699

Heteroptera Families

	Nepidae		**Micronectidae**		**Notonectidae**		**Gerridae**		**Veliidae**		**Hydrometridae**	
Factor	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***	**F**	***p***
Sampling Period	1.520	0.220	0.638	0.594	3.134	**0.033**	4.345	0.**008**	0.660	0.581	0.849	0.474
Pond Type	10.953	**0.004**	0.546	0.470	0.389	0.551	0.003	0.956	0.918	0.351	0.400	0.535
Interaction	1.765	0.166	0.958	0.420	0.704	0.554	0.310	0.585	2.547	0.066	0.483	0.696

Coleoptera Families

	Dytiscidae		**Hydrophilidae**	
Factor	**F**	***p***	**F**	***p***
Sampling Period	3.127	**0.034**	2.172	0.103
Pond Type	0.861	0.366	0.065	0.801
Interaction	0.621	0.605	1.013	0.395

Diptera Families

	Culicidae		**Chironomidae**	
Factor	**F**	***p***	**F**	***p***
Sampling Period	2.722	0.054	3.480	**0.022**
Pond Type	0.151	0.702	0.001	0.973
Interaction	0.507	0.679	1.149	0.338

[a]significant *p* values are in bold

hurdle to maintaining membership in the community, as predicted in the interactive phase of community development from island biogeography theory (Simberloff & Wilson, 1969, 1970; Wilson & Simberloff, 1969). As densities and richness rose, some species were excluded by predation and competition, but the taxa most likely to be excluded were dependent on which predators or competitors had already taken up residence. The specific immigration and extinction events preceding the recovering community at any point in time were not random, but were predictable only in a general sense. From a taxonomic perspective: The assembly of the community at the ordinal level is far more predictable (and hence less stochastic) than at the species level. As such, a quasi-stochastic series of events controlled the direction of community assembly. Further, because so many of the genera were represented by multiple species, substantial overlap in ecosystem function undoubtedly was represented by congeners, thereby imparting a high degree of community resilience (e.g., Peterson et al., 1998). How the abiotic conditions and biotic interactions would shape the community could have moved in one of three directions: First, the community could have been limited to and maintained in its early taxonomic composition as controlled by powerful environmental constraints associated with proximity to the ocean (e.g., conductivity, salinity). Second, the community could have evolved toward the end-state composition

Table 5. Discriminant function analysis structure matrix with factor loadings for each of three axes using order richness values as independent variables. Asterisks indicate loadings most important for that particular function.

Richness Variable	FUNC 1	FUNC 2	FUNC 3
Hemiptera	0.79604*	0.08275	-0.59956
Coleoptera	0.41353*	-0.27457	-0.18051
Odonata	0.39623	0.90745*	0.13981
Ephemeroptera	0.06009	0.15838*	0.05156
Diptera	0.68100	-0.17856	0.71018*
eigenvalue	0.6453	0.1250	0.0159
percent variance	82.08	15.90	2.02

represented by the community in the nearby unaffected ponds, as can be documented effectively by parsimony analysis (Wenzel & Luque 2008). Third, a growing body of literature suggests the most likely scenario is that the post-impact community follows an assembly trajectory that will result in a community unlike that of either pre-impact or unimpacted reference communities, but to one of multiple alternative stable states (e.g., May, 1977, 2001; Beisner et al., 2003).

Our first samples were taken in May 2005, approximately five months following the tsunami. By that time, a substantial insect community had already taken residence during the dry season. At the ordinal level, the slowest to colonize the inundated ponds was Ephemeroptera, as evidenced by significantly lower richness ($p = 0.009$) between pond types (Table 4). Ephemeroptera are well known to be weak fliers (Dudgeon, 1999), some of which exhibit seasonally timed emergence patterns, although emergence patterns in the tropics are more staggered than in temperate regions (Ghee, 2004). In sharp contrast, the first pond that we sampled had abundant exuvial evidence that a generation of Libellulidae (Odonata) had already gone through the larval stage of their life cycle. The discovery of odonate exuviae in inundated ponds five months after the tsunami is not surprising. Odonata are powerful fliers and have been considered to include taxa more salt tolerant than many other aquatic macroinvertebrates (Kefford et al., 2004), although considerable variation in tolerance exists within the order (Gooderham & Tsyrlin, 2002; Chessman, 2003; and Morris et al., 2009). Our inability to identify most odonate immatures even to generic level underscores the clear need for taxonomic research of immature Odonata in Southeast Asia.

Many taxa of other aquatic insect groups can withstand or even flourish in relatively high levels of salinity. *Culex sitiens* Wiedemann, which we collected only from inundated ponds, occurs in salinities up to 115% that of seawater with peak abundance in 80% seawater salinity (Roberts & Irving-Bell, 1997). We collected other species of mosquito larvae exclusively from tsunami-inundated ponds, including *Anopheles epiroticus* (Linton & Harbach),

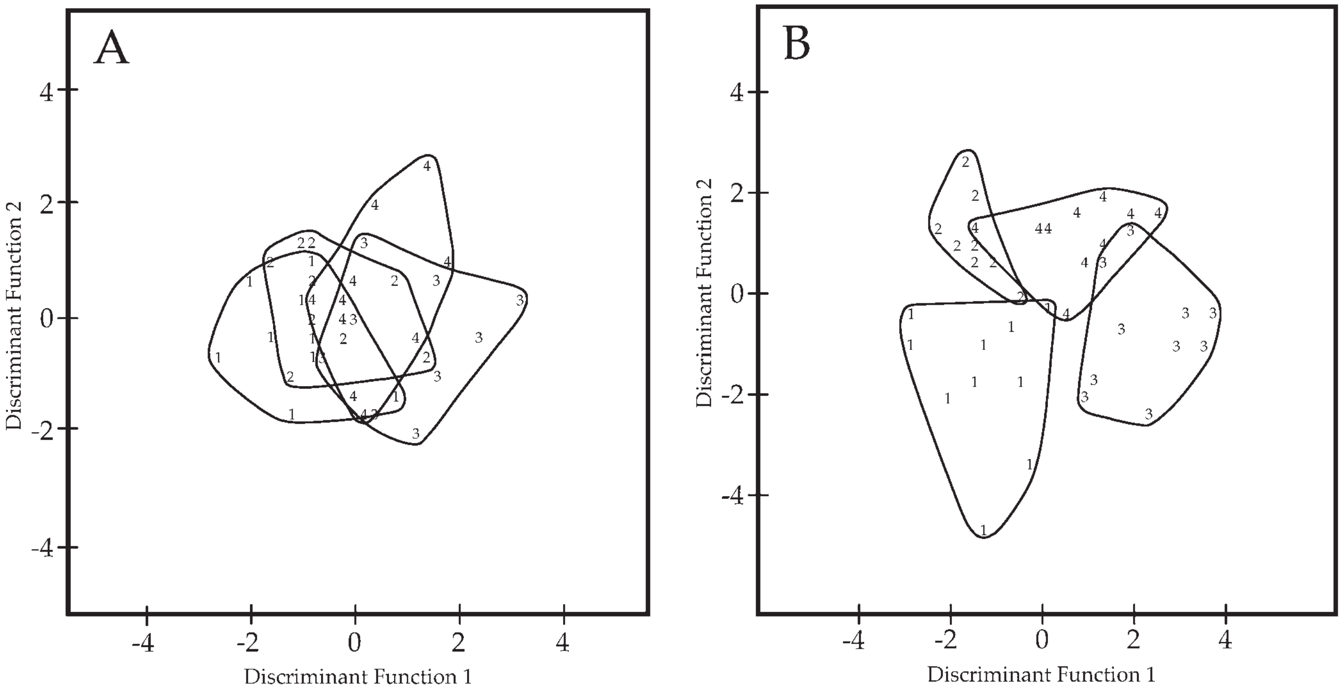

Fig. 4. Discriminant Function Analysis with group contour limits for each of four sampling periods of tsunami-inundated ponds using (A) ordinal and (B) family richness values.

A. barbirostris van der Wulp, and *Culex vishnui* Theobald, suggesting salt tolerance in these species. The larvae of *Culex tritaeniorhynchus* Giles, another species of mosquito, was found predominantly in inundated ponds, although it was taken also in one unaffected pond with low conductivity (62.7 µS). This species was reported to have peak abundance in water with salinity 30% that of seawater (Roberts & Irving-Bell, 1997). A number of these and other mosquito taxa represented in our samples occur in saline conditions in Thailand, including *Anopheles barbirostris* van der Wulp, *A. epiroticus* (Linton & Harbach), *Culex sitiens* Wiedemann, *C. tritaeniorhynchus* Giles, and *Verrallina* (Rattanarithikul et al., 2005a, b; 2006).

Insects arrive within days or even hours following inundation of seasonally dried basins (Hall et al., 2004; Batzer et al., 2006). In fact, some mosquitoes, midges, dragonflies, and beetles have been documented to oviposit in wetlands as they become inundated (e.g., Streever et al., 1996; Brown et al., 1997; Mitsch et al., 1998; Keiper & Walton, 2000; Wrubleski, 2005). The source bodies of water providing the inoculum of immigrant individuals to the defaunated ponds are abundant and scattered throughout the area. Some lentic species of the Isthmus of Kra are well-adapted for occurrence in temporary ponds since they are prevalent in rice agroecosystems, which flood and dry episodically. Thus, the local source fauna includes many species that disperse quickly to newly available bodies of water. As the seawater in the ponds inundated by the tsunami recharged to freshwater and limiting environmental constraints changed to allow survival, the dispersing insect pressure ensured rapid recolonization.

Recovery of a biotic community following a catastrophic event is a process of decent with modification, in a similar sense to the same concept in phylogenetics (Wenzel & Luque, 2008). The community at one point in time gives rise to the community at a later point in time. As such, some species are added and others removed as the taxonomic composition and density move toward that of a more stable community. Thus, as communities re-establish following extirpation, they can be considered to be ‘evolving’ toward a state in which particular species will generally be present in equilibrium with other species. The pathway that these communities follow to arrive at this state can be estimated using the same quantification that is used in parsimony analysis. However, the dendrogram (Fig. 5) did not reveal a clear successional pathway toward the community represented by the unaffected control ponds. Rather, it resulted in several tangential trajectories, indicating that these ponds might be progressing toward alternate stable state communities with faunistic attributes other than those represented by the control ponds. Attempting to define environmental characteristics in common among the ponds within each pathway is not feasible, as many confounding characteristics are involved. Moreover, factors including conductivity, acidity, background salinity, pond size, depth, vegetation presence and type, substrate type, proximity to other ponds, and watershed characteristics play a role in shaping the taxonomic composition of the immigrant community, and affect assembly of the community at any point in time (see Diamond, 1975). A further confounding factor is that unlike the inundated ponds, the fauna of most unaffected ponds probably included fish, which are known to selectively prey on particular insect food items (e.g., Bendell & McNicol, 1987; McPeek, 1990a, b). As such, presence or absence of fish would have had an effect on succession and community re-establishment.

The tangential successional pathways are characterized by the common presence or absence of particular taxa that removes them from the primary pathway (represented by the stepwise ladder on the right side of the dendrogram). It is possible that as environmental conditions change, key species will be added or lost that will move the community back to the primary pathway leading to the communities represented by the control ponds. However, we consider it likely that the tangential pathways will lead to stable equilibrium communities with taxonomic composition substantially different from that of the control communities, particularly if environmental conditions remain different from those of the control ponds (e.g., continued higher conductivity levels and absence of fish predators). Whether or not the tangential pathways ultimately result in taxonomic composition of control ponds or that of an alternative stable state would require continued sampling to follow community succession for a longer period of time.

The concept that the tangential pathways might not be leading to control communities in the parsimony analysis is supported by the similarity analyses and subsequent cluster dendrograms. On each of the four sampling dates and overall, fidelity of pond type based on the taxonomic composition is clear, suggesting that the community in the inundated ponds has not demonstrated any signs of shifting toward that of the unaffected control ponds. So, although we see little difference between pond types based on species richness (see Table 4), analyses based on taxonomic composition tell a different story; that the insect fauna in the inundated ponds continues to differ dramatically from that of the unaffected ponds.

The studied peat swamps were bodies of water of substantially greater diameter and depth than were the ponds in this study. Several of the taxa that Watanasit (1995) listed from the peat swamps probably were misidentified. Because we collected no specimens of Siphlonuridae in any sample during this study, and this family is unknown from southern Thailand, including Phuket (Sites et al., 2001), Watanasit’s specimens of Siphlonuridae probably were actually a large baetid. Macroveliidae is known only from the New World (Schuh & Slater, 1995), thus, Watanasit’s record was most likely in reference to *Neoalardus typicus* (Distant), a veliid of superficial morphological similarity. His specimens of Corduliidae (Odonata) were probably Macromiidae, which was previously considered a subfamily within Corduliidae. Although he did not mention the genus of Corixidae in his collections, these were probably *Micronecta*, which has now been placed in the family Micronectidae, following subfamily elevation. Because our richness and abundance values were drastically lower than those of Watanasit, this suggests that the communities of the peat swamps might

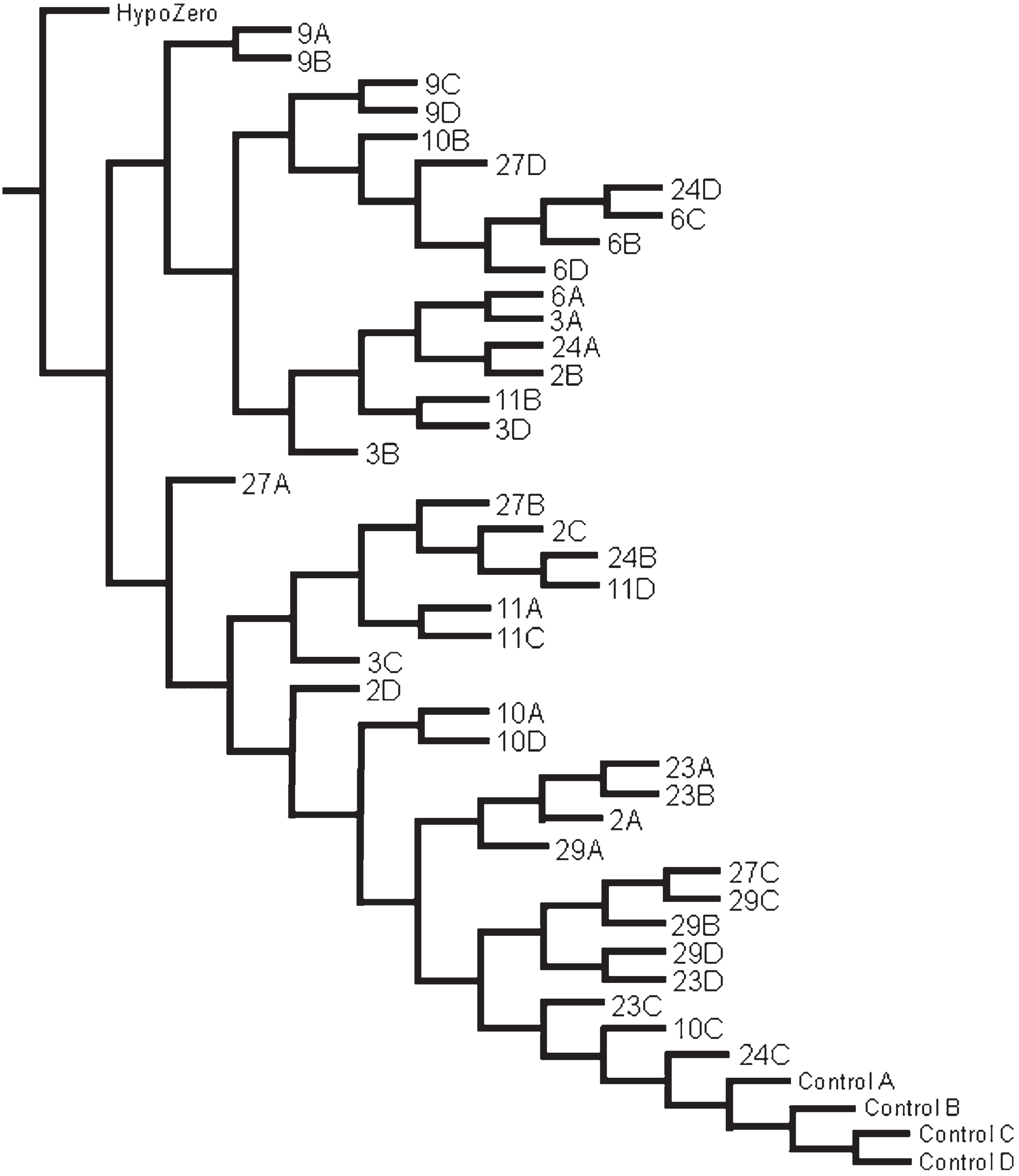

Fig. 5. Parsimony dendrogram showing succession of 10 sites (ponds) over 4 sampling periods toward the fauna of unaffected control ponds. Site numbers correspond with numbers in Table 1 and Figure 1. Letters A–D following site numbers refer to sampling periods 1–4.

Table 6. Discriminant function analysis structure matrix with factor loadings for each of three significant axes using family richness values as independent variables. Asterisks indicate loadings most important for that particular function.

Richness Variable	FUNC 1	FUNC 2	FUNC 3
Ceratopogonidae	0.35683*	0.16128	0.14550
Gerridae	0.28313*	-0.10042	0.11324
Notonectidae	0.26304*	0.04657	-0.11326
Belostomatidae	0.22028*	0.13158	-0.15139
Scirtidae	0.20945*	-0.01567	0.02271
Dytiscidae	0.20859*	0.01249	-0.10860
Pleidae	0.16010*	0.06201	0.06647
Gyrinidae	0.14599*	0.06666	0.07409
Hydraenidae	0.14508*	0.04352	0.01229
Hebridae	0.14186*	-0.12909	-0.12390
Culicidae	0.19824	-0.28368*	-0.09936
Chironomidae	0.02279	0.28046*	0.05646
Haliplidae	-0.01653	-0.27695*	-0.03277
Anisoptera	0.06143	0.26918*	0.11590
Mesoveliidae	0.03688	0.23147*	0.12703
Hydrometridae	0.05560	0.21139*	0.06496
Naucoridae	0.12875	-0.19577*	0.01710
Hydrophilidae	0.07506	-0.18297*	0.09552
Micronectidae	-0.11389	0.17612*	-0.12090
Nepidae	0.02140	0.16087*	-0.04058
Veliidae	0.05260	0.11018*	-0.04037
Caenidae	0.05852	0.09724*	0.06408
Tabanidae	0.12855	0.00496	0.45292*
Zygoptera	0.24987	0.15550	-0.28360*
Baetidae	0.16581	-0.15531	0.16684*
Stratiomyidae	0.07815	0.02866	0.08212*
eigenvalue	2.4896	1.7373	0.6886
percent variance	50.65	35.34	14.01

require an even greater time for recovery than the do the pond communities. This could be because environmental conditions altered by the tsunami persist for a longer period of time, thereby acting to limit the establishment success of immigrating taxa. The larger, deeper bodies of water require a longer period of time to recharge to freshwater, and our conductivity measurements indicate that even at the fourth sampling period, levels remained higher (mean: 7,668 µS) than for the inundated ponds. Anthropogenic habitat disturbance was ongoing by the diverting of water from the peat swamps to artificial shrimp ponds as a rapid means of adaptation by local people for economic recovery after the tsunami. In addition, a reduced rate of immigration might have existed because the peat swamps are situated near the northern end of Phuket Island and thus are bounded by ocean on two sides, an airport, and residential housing. Thus, the source communities for recolonization of the peat swamps are more distant than for the ponds in our study. This hypothesis is supported taxonomically by the depauperate culicid and chironomid faunas in our samples. These insects are weak fliers, and although they were in the ponds quickly, including ponds with high conductivity levels, they still were absent from the peat swamps, although the depauperate odonate fauna is confounding.

Hemipterans of the genus *Micronecta*, which are strong fliers and readily come to lights and reflective surfaces, established quickly in the peat swamps. These insects are known to tolerate bodies of water with elevated salinity (Knowles & Williams, 1973) and we collected seven species from the peat swamps with conductivity as high as 12,350 µS, and 9 species from inundated ponds, also with various elevated levels of conductivity.

Because of their tolerance to saline conditions, ubiquitously high levels of diversity, and propensity for rapid colonization, Chironomidae and Micronectidae appear to represent insect taxa with promising utility as indicators of graded saline conditions in Southeast Asia. These families already have known utility as water quality indicators. The Chironomidae is well established as a family of very effective water quality indicators (e.g., Saether, 1979), and is frequently

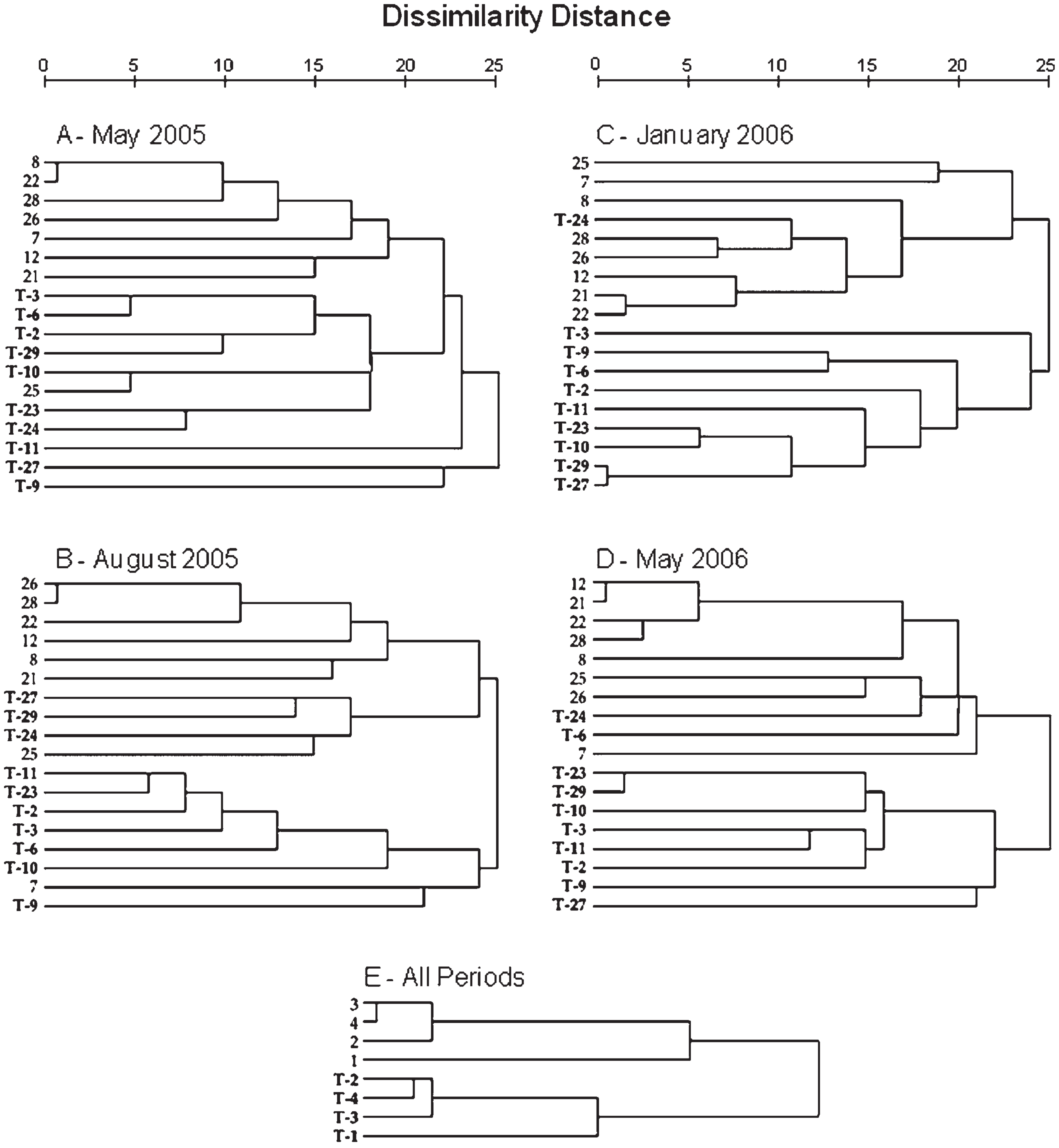

Fig. 6. Cluster analyses based on similarity in the taxonomic composition of the insect fauna as estimated by Jaccard's similarity index. A–D, tsunami-inundated and unaffected ponds within each sampling period separately. Inundated ponds are indicated with a "T" and boldface, site numbers correspond with numbers in Table 1 and Figure 1. E, similarity in taxonomic composition among sampling periods (1–4), with ponds pooled within period. Inundated ponds are indicated with a "T" and boldface.

Table 7. Abundance of taxa(a) collected in peat swamps inundated by the tsunami of 2004. Pre-tsunami wet and dry season data from samples of 1994 and 1995 (Watanasit 1995) are in comparison with post-tsunami samples of 2005 and 2006.

Taxon	Wet 94	Wet 05	Dry 95	Dry 05	Dry 06
COLLEMBOLA					
Entomobryidae	0	0	1	0	0
EPHEMEROPTERA					
Baetidae	747	5	112	0	1
Caenidae	22	0	0	0	4
ODONATA					
Zygoptera					
Protoneuridae	12	1	3	0	0
Lestidae	2	0	8	0	0
Coenagrionidae	12	1	4	0	0
Anisoptera					
Libellulidae	68	4	49	1	7
Gomphidae	1	0	7	0	0
Aeshnidae	0	0	1	0	0
Macromiidae	26	20	0	0	3\
HEMIPTERA					
Belostomatidae	96	6	28	0	1
Micronectidae	297	66	224	50	12
Gerridae	27	13	1	8	1
Nepidae	25	1	0	3	1
Notonectidae	100	25	36	5	1
Mesoveliidae	27	0	8	0	2
Pleidae	37	0	172	0	0
Veliidae	23	0	8	0	0
Hydrometridae	1	0	7	0	1
NEUROPTERA					
Sisyridae	1	0	0	0	0
DIPTERA					
Ceratopogonidae	1	0	0	0	0
Chironomidae	0	0	283	0	0
Culicidae	389	0	337	3	11
Tipulidae	0	0	34	0	0
Tabanidae	3	0	1	0	0
LEPIDOPTERA					
Pyralidae	8	0	0	0	0
TRICHOPTERA					
Limnephilidae	7	0	0	0	0
Unknown family	1	0	0	0	0
COLEOPTERA					
Gyrinidae	1	0	0	9	0
Noteridae	53	0	91	0	0
Dytiscidae	6	1	97	5	1
Haliplidae	5	0	1	0	0
Hydrophilidae	50	2	35	4	1
Scirtidae (=Helodidae)	1	0	0	0	0

[a] See Table 2 for finer identifications of insects collected in 2005 and 2006. We consider several of Watanasit's taxa to actually represent other families as follows: Siphlonuridae is Baetidae, Corduliidae is Macromiidae, Macroveliidae is Veliidae. The subfamily of Corixidae represented in Watanasit's study has been elevated to Micronectidae.

included in various metrics and indices of biotic integrity. The Micronectidae has been suggested by Jansson (1977a, b; 1987) as an indicator group for levels of industrial pollution and eutrophication. The use of species of *Micronecta* to indicate levels of salinity represents an extension of Jansson's concept, one worthy of future research. Tolerance to salinity in general appears to be greater and taxonomically more widespread than previously considered and is worthy of further research.

In summary, the ponds inundated by the tsunami were colonized quickly by taxa with high salt tolerance, including some Libellulidae (Odonata) and Culicidae (Diptera). Other groups arrived later during freshwater recharge and their survival and persistence were controlled by changes in constraining environmental attributes as well as biotic interactions. Ephemeroptera was the slowest order to colonize the inundated ponds. As such, distinctly different communities became established quickly, and the trajectory of assembly suggests that the communities ultimately achieved will be of an alternative taxonomic composition to that represented by the nearby unaffected ponds.

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