Spatial ecological approach to evaluating the potential of immigration of dragonflies to newly created habitats

（新たに創出された生息場所へのトンボ類の移入ポテンシャルに関する空間生態学的評価）

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Taku KADOYA

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Chapter 1 General Introduction

General backgrounds

Biodiversity is defined as "the variability among living organisms from all sources including, interalia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part" (Convention on Biological Diversity 1992) and composed from several levels such as diversity within species, between species and of ecosystems (Noss 1990). Biodiversity provides a wide range of significant use and nonuse benefits and essential life-support services (i.e., ecosystem service), which are indispensable to maintain sustainable human society (Millennium Ecosystem Assessment 2004). However, biodiversity have declined steeply both at global and regional scales due to habitat destruction and fragmentation, pollution, over-exploitation, biological invasion, climate change, and so on (Millennium Ecosystem Assessment 2004).

Currently, in the face of the rapid biodiversity loss, biodiversity conservation is becoming an international urgent issue, and the 2002 World Summit on Sustainable Development (WSSD) endorsed the Hague Ministerial Declaration of the Sixth Conference of the Parties to the Convention of Biological Diversity (CBD) in its Plan of Implementation, that is, "to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to proverty alleviation and to the benefit of all life on earth." (United Nations 2002). In the new National Biodiversity Strategy of Japan approved in 2002 based on CBD's provisions, it is also aimed to

"reinforce the protected-area system, expand the designation of protected areas, improve conservation and management activities based on scientific data" and "promote the restoration of nature by having human beings assist with natural restoration processes through launching of nature restoration projects" in order to prevent species extinction and conserve the biodiversity (Ministry of the Environment of Japan 2002b).

In order to prevent the loss of biodiversity and to achieve progress toward this objective, governments and intergovernmental organization will need to monitor the biodiversity to acknowledge how well they are doing. The biodiversity monitoring will require a series of standardized, regularly repeated measurements of the state of biomes and their biota. These measurements must capture information on the area of biomes: the diversity, distribution, and abundance of species (e.g., Ceballos & Ehrlich 2002); and the provision of ecosystem goods and services. It is clear, however, that there is a great deal of work to be done before the scientific community can generate reliable time series of data relevant to this target for wide range of biomes and attributes at the global level (Green *et al.* 2005; Pereira & Cooper 2006).

Modeling the distribution of indicator species

In the face of limited funding, knowledge, and time for action, conservation efforts often rely on shortcuts for the maintenance of biodiversity (i.e., indicator). Indicators are measurable surrogates for environmental end points such as biodiversity conservation that are assumed to be of value to the public (Niemi & McDonald 2004). Ideally, an indicator should be (1) sufficiently sensitive to

provide a nearly warning of change; (2) distributed over a broad geographical area, or otherwise widely applicable; (3) capable of providing a continuous assessment over a wide range of stress; (4) measurable as simple as possible (Noss 1990).

Because of its hierarchical nature, biodiversity should be monitored at multiple levels of organization, and at multiple spatial and temporal scales (e.g., Bani *et al.* 2006; Pereira & Cooper 2006). No single level of organization (e.g., gene, population, community) is fundamental, and different levels of resolution are appropriate for different questions(Niemi & McDonald 2004). In particular, however, the population-species level is where most biodiversity monitoring has been focused for two basic reasons: (1) species are often more tangible and easy to study than communities, landscapes, or genes; (2) laws such as the U.S. Endangered Species Act (ESA) mandate attention to species but not to other levels of organization (Niemi & McDonald 2004).

Noss (1990) lists five categories of species that may warrant special conservation effort, including intensive monitoring (1) ecological indicators: species that signal the effects of perturbations on a number of other species with similar habitat requirements; (2) keystones: pivotal species upon which the diversity of a large part of a community depends; (3) umbrella: species with large area requirements, which if given sufficient protected habitat area, will bring many other species under protection; (4) flagships: popular, charismatic species that serve as symbols and rallying points for major conservation initiatives; and (5) vulnerables: species that are rare, genetically impoverished, of low fecundity, dependent on patchy or unpredictable resources, extremely variable in population density, persecuted, or otherwise prone to extinction in human-dominated

landscapes. Especially, the umbrella species concept has recently received growing attention (Fleishman *et al.* 2001; Fleishman *et al.* 2000; Roberge & Angelstam 2004). In addition, the concept has been extended to include not only area-limited species but also species limited by other landscape attributes such as habitat connectivity, the occurrence of various ecosystem process, or the distribution of scarce resources (Lambeck 1997).

Monitoring at the population-species level should be focused on certain trends in the abundance and distribution of populations of indicator species (Balmford *et al.* 2005). If the status of indicator species can be captured and monitored regularly, it may be possible to determine how current conservation efforts can be improved and to guide new strategies. For example, we can identify hotspots of biodiversity or prioritize areas where populations are most likely to persist in the long-term at larger spatial scale (e.g., Moilanen *et al.* 2005).

However, survey work to monitor the species' status directly at larger spatial scale can be very expensive and sometimes not feasible. Therefore, the monitoring is often directed not at the population itself, but at their abiotic or biotic environments determined or assumed to be important to the species, and through modeling the relationships between these habitat variables and the distribution of target species (Rushton *et al.* 2004). The collection of habitat data for species distribution modeling underwent dramatic change in the 1990s when remote-sensed imagery derived from satellites became widely available. This, couple with the increased use of geographical information systems (GIS) to store and manipulate spatial data, led to an expansion in species distribution modeling (Guisan & Zimmermann 2000).

Recently, while there has been an ongoing interest in the development and application of modeling approaches, the last a few years have seen fundamental changes in the methodology involved with this form of modeling. The distribution modeling based on information-theoretic approaches has been getting popularity, coupled with the generalized linear modeling (GLM) (Rushton *et al.* 2004).

The standard method for assessing all linear models is to test the null hypothesis, that the regression coefficients estimated from the model are no different to zero. When there are many potential predictor variables, which is a common feature of much species distribution modeling, model selection is usually based on stepwise consideration of variables (Whittingham *et al.* 2006), and reliance on hypothesis testing forces ecologists into a decision-making approach focusing on arbitrary levels of statistical significance (Johnson 1999), and then, the model with the least residual deviance is selected as the best. It is possible to overfit models to the extent that they appear to explain variation in the observed dataset, but perform poorly when used in other circumstances (Johnson & Omland 2004).

On the other hand, the information-theoretic approach is based on formulating a series of models that rely on an understanding of the system being studied, following by an assessment of how the different putative model(s) compare(s) to reality (Johnson & Omland 2004). The scientist selects the model (or possibly a small set of models) that is nearer to reality than any of the rest. The basis for comparing candidate models is Akaike's Information Criteria (AIC). The AIC can be used to determine Akaike weight for each model, which are the

weights of evidence in favor of each model being the nearest to reality, given the other models being considered (Burnham & Anderson 2002). The most obvious feature of this approach is that it is comparative, and leads to the identification of the best amongst a suite of models. More importantly, inference and prediction need not necessarily be based on one (the best) model. Where there are several alternative models, each supported by the data, then the suite of good models should be used in inference and prediction using multi-model inference, or model-averaging approach in which the relative importance of each parameter is calculated as the sum of the Akaike weights over all of the models in which the parameter of interest appears (Anderson *et al.* 2000; Burnham & Anderson 2002; Johnson & Omland 2004).

The preparation of a model of the system is an important intermediate step before collecting data because the development of even a simple conceptual model forces assumptions to be recognized and made explicit and highlights defects in the reasoning linking the attributes of interest to the measurements that can be made, and helps specify exactly what, when, where, and how to measure the data (Green *et al.* 2005). After data sampling and analyses using the model, the sensitivity of the conclusions of the evaluation to the underlying model and its assumptions should be explored and reported clearly and the result of the study should be used to update the underlying model of the system as a basis for future evaluations (Green *et al.* 2005). Defects in the model should be identified clearly and remedies should be suggested as needed. These steps will create a dynamic cycle with feedback loops between data collection and model prediction, and help increase reliability of model structures and predictions.

Monitoring of immigration potential

A set of local populations that are linked by dispersal of individuals (species) forms metapopulation (Hanski 1999). Similarly, a set of local communities that are linked by dispersal of individuals forms metacommunity (Leibold *et al.* 2004). In such a system with meta-structures, or hierarchy, higher levels of organization incorporate and constrain the behavior of lower levels (O'Neill *et al.* 1986). Local population dynamics are quantitatively affected by dispersal from the meta-level (i.e., rescue effect or mass effect). The role of dispersal of individuals between local populations or communities is twofold. First, immigration can supplement local birth rates to enhance densities of local populations beyond what might be expected in closed populations (communities) and second, emigration can enhance the loss rates of local populations from that expected in closed populations (communities) (Brown & Kodricbrown 1977; Holyoak & Ray 1999; Shmida & Wilson 1985). In this manner, dispersal process links local populations or communities, and causes the spatial dependence of dynamics and distribution of species over landscapes beyond the constraints by local environmental factors. Therefore, in such situation, dispersal process would be better to be considered explicitly in a distribution model as well as local habitat variables to make rigorous predictions.

Modeling dispersal process will make it possible to estimate the immigration potential of individuals (or species) to local habitats at landscape. Immigration potential is defined as 'expected ease of colonization' to a habitat for individuals (or species) as a function of connectivity, which is defined as "the

degree to which the landscape facilitates or impedes movement among resource patches" (Taylor *et al.* 1993), and source size at meta-level. Immigration potential of individuals has been revealed to determine the proneness to extinction of local populations, and consequently have significant effects on metapopulation viability (Hanski 1999). Immigration potential of species also play an important role in determining the species diversity at local communities (Cadotte 2006; MacArthur & Wilson 1967) and metacommunity dynamics (Koelle & Vandermeer 2005). Therefore, to know the distribution and magnitude of immigration potential at landscape would be one of fundamental measures to monitor the dynamics of populations and communities, or to predict the recovery potentials of species at a restored habitat.

Spatial ecological approach to capturing the immigration potential

In spatial modeling including, modeling of species distribution, the problem of spatial autocorrelation often arises. Spatial autocorrelation may be loosely defined as the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observation (Legendre 1993). Autocorrelation in a variable brings with it a statistical problem: it violates the assumption of independence among observations, and impairs our ability to perform standard statistical test of hypotheses. In classical statistical testing, one counts one degree of freedom for each independent observation, and this procedure allows one to choose the statistical distribution appropriate for the given test. Under the presence of

autocorrelation, new observations do not each bring with them one full degree of freedom. Positive autocorrelation between two variables, for example, induces the bias that computed correlation coefficient is too often declared significantly different from zero (Legendre 1993). The problem of spatial autocorrelation has been recognized relatively recently in the area of ecology, and the new theory and techniques to treat the spatial autocorrelation have been developed rapidly for the last decades (Fortin & Dale 2005; Wagner & Fortin 2005), which includes variation partitioning analysis coupled with trend surface analysis (Borcard *et al.* 1992), autoregression analysis (Augustin *et al.* 1996) and generalized linear spatial model (Christensen & Waagepetersen 2002).

Spatial structure, however, is often functional in ecosystems, and not the result of some random, noise-generating process (Borcard *et al.* 1992; Legendre 1993), so it becomes important to study the spatial autocorrelation to capture the pattern generating process such as dispersal and species interaction. Especially, when the available data are scares, information about such processes hidden in the spatially autocorrelated pattern would be valuable.

The approach to including the connectivity or dispersal in more explicit manner is often adopted in empirical distribution modeling. Negative-exponential form is frequently used to model the random dispersal of organisms (Turchin 1998) and connectivity between habitats (Moilanen & Nieminen 2002). Rhodes et al. (2006), for example, to model the distribution of Koala, used distance weighted metrics as explanatory variables in generalized linear mixed model. The metrics were weighted means of values of the landscape variables such as natural habitats for Koala or fire frequency around sampling site, with an exponential

decline in weighting with distance from the site. Moilanen et al. (2005) calculated population connectivity surfaces of individual species, and used these as a basis for zoning (prioritizing) landscapes for multi-species conservation. In their study, the connectivity was also modeled as weighted sum of source patch size by an exponential decline in weighting with distance between patches. The variables related dispersal and connectivity such as the distance-weighted metrics may produce much better and more biological meaningful models in prediction than simple model which considers only local habitat variables, especially when the target species dispersed between habitats more or less.

Bottom-up modeling approach using simulation models based on individual behavior rules or ecological processes, which are empirically known, provide powerful tools to predict dynamic changes of abundance and distribution of target species (Grimm & Railsback 2005). In conservation ecology, during the 1980s population viability analysis (PVA) became an important tool in assessing the likelihood of a population becoming extinct and PVAs have subsequently been used to aid management decisions about threatened species (Beissinger & McCullough 2002). Despite the growing use of simulation models in conservation ecology, early enthusiasm has been tempered by the following problems: (1) the inherent lack and uncertainty of data, especially on endangered species, (2) the complexity of realistic simulation models, (3) problems of error propagation (Ruckelshaus *et al.* 1997), (4) missing criteria for aggregating the biological information, and (5) difficulties in testing model predictions (Wiegand *et al.* 2003). Especially, because traditional measurement of parameter values relies heavily on data obtained from a low hierarchic level of population dynamics, such

as mortality rates, model predictions are usually quite sensitive to uncertainty in the data.

In principle, spatially-explicit and individual-based simulation models are able to include many biological details and may contain many parameters. This can be problem, not only because of error propagation or lacking direct estimates of model parameters, but also because their complexity may prevent an exhaustive model analysis. Recently, to overcome these problems, Grimm and colleagues proposed "pattern-oriented modeling" approach (Grimm *et al.* 2005; Wiegand *et al.* 2003). The basic idea for the approach is to include in the model the constraining factors and the minimal set of processes that are necessary for reproducing the patterns and to systematically compare the observed patterns with the patterns produced by different modifications in the structure and/or the parameterization of the model. A pattern is anything that goes beyond random variation and thus indicates underlying processes that generate this pattern (Levin 1992). Such patterns include time-series trends of population dynamics (Wiegand *et al.* 2004b), the distribution of dispersal distance and the spatial pattern of species occurrence in fragmented landscape (Hanski 1994). Such patterns represent high-level manifestations of population dynamic processes and the outcome of interplay between demographic processes, dispersal characteristics and various constraining factors (e.g., management actions, or a climate pattern). Therefore, empirically observed patterns contain a great deal of information and memory about the history of the system.

Because the patterns describe features of the system at a higher hierarchic level than are addressed by possible model rules, there are only limited

possibilities to include this information directly into the rule set of a model (Grimm & Railsback 2005). Unfortunately, indirect methods of parameter estimation, a standard practice in many areas of science, which would allow the use of the 'hidden' information, are widely overlooked in conservation (Wiegand *et al.* 2003). Under circumstances of scarce data, common situation in conservation biology, the additional data provided by independent patterns may be especially valuable and could greatly improve the quality of model predictions and the general understanding of the system.

Biodiversity in agricultural habitat complex

Cultivated systems (areas where at least 30% of the landscape is in croplands, shifting cultivation, concerned livestock production, or freshwater aquaculture) now cover one quarter of Earth's terrestrial surface (Millennium Ecosystem Assessment 2004). The loss of semi-natural habitats due to agricultural intensification and marginalization of traditional agricultural systems, both of which have led to the abandonment of traditional land uses, is one of the main threats to biodiversity in agricultural ecosystems (Krebs *et al.* 1999; Ormerod *et al.* 2003). In addition, while the expansion of agriculture and its increased productivity is a success story of enhanced production of one key ecosystem service, this success has come at high and growing costs in terms of trade-offs with other ecosystem services, both through the direct impact of land cover change and as a result of release of nutrients into rivers and water withdrawals for irrigation (Millennium Ecosystem Assessment 2004).

In the Japanese archipelago, the abundant rainfall and generally mild

temperatures throughout most of the country (Yoshimura *et al.* 2005) produce a lush vegetation cover and enable a variety of crops to grow, except over mountainous terrain or in waterlogged regions. The monsoon climate with frequent typhoon landings (Chen *et al.* 2004) and high volcanic, seismic and geomorphic activity cause frequent natural disturbance such as landslides, fires, winds and flooding, which destroy established vegetation in various spatial and temporal situations, and enhance regional or local environmental heterogeneity. Such natural conditions promote high biodiversity, despite Japan's small land area of about 378000 km^2 (Ministry of the Environment of Japan 2002b).

Satoyama, which was a common rural agricultural ecosystem before the westernization of Japanese communities, consisted of a mosaic of patches of forests, grasslands, ponds and creels supplying various resources to support traditional agriculture and village life (Kobori & Primack 2003; Washitani 2001). The landscape mosaic of Satoyama provided a variety of habitats for wild animals and plants, and contributed to high inter-habitat diversity (Takeuchi *et al.* 2003). Moderate disturbance and stresses associated with exploitation of plant materials from coppice forests and grasslands, i.e. clearing, mowing, coppicing, burning and litter removal, prevented competitive exclusion by a few dominant species and enhanced intra-habitat diversity (Fukamachi *et al.* 2001; Washitani 2001). In addition, in Japan, where rice is a staple food, the aquatic habitat complex, the network of paddy fields, ponds, and creeks, which are connected to adjacent rivers or streams, provided various habitats for a number of aquatic organisms including plants, invertebrates, fish, and amphibians (e.g., Mukai *et al.* 2005; Takeda *et al.* 2006).

Abandonment of Satoyama ecosystems, which had lost their instrumental value mainly due to the fuel revolution and popularization of chemical fertilizer use, and their destruction due to regional development projects during periods of rapid growth and the bubble economy resulted in the loss of various types of habitats constituting traditional rural landscapes (Fukamachi *et al.* 2001) and have caused the serious threats to many plant and animal species including those which were among the most familiar to people several decades ago (Washitani 2001). According to the Red Data Books/Red Lists which the Ministry of the Environment revised, 669 species of animals and 1994 species of plants are categorized as threatened (endangered and vulnerable) (Ministry of the Environment of Japan 2001), most of them used to be very common in rural agricultural ecosystems. Therefore the conservation of biodiversity and restoration of heterogeneous habitat complex in rural agricultural ecosystem have become an urgent matter in conservation. In addition, to archive these objectives, effective techniques and schemes for biodiversity monitoring are needed.

Study species

Dragonflies have been widely proposed as indicators of the ecological quality of land–water ecotones, aquatic habitat heterogeneity (e.g., bank morphology and aquatic vegetation), and the hydrological dynamics of water bodies (e.g., Chovanec & Waringer 2001; e.g., Clark & Samways 1996; D'Amico *et al.* 2004). They have complex life cycles, shifting from aquatic to terrestrial habitats in their adult stage, thus during their pre-reproductive phase at adult stage, individuals are compelled to move between two types of habitats, from aquatic areas to terrestrial

areas and back again. Pre-reproductive phase dragonflies of many species use woodlands or forests as suitable habitats for foraging, resting, and avoiding unsuitable (dry or hot) conditions (e.g., Fincke 1992; Morton 1977; Watanabe *et al.* 2005). Therefore it is likely that they needs complex of both aquatic and terrestrial habitats to maintain viable populations.

In Japan, there are about 200 resident dragonfly species constituting one of the major taxa inhabiting the traditional rice agricultural ecosystem in Japan (Sugimura *et al.* 1999). The dragonflies are an insect group Japanese are especially fond of (Primack *et al.* 2000) and their ecological characteristics such as behavior and habitats were thoroughly described by a number of enthusiasts including amateurs (e.g., Sugimura *et al.* 1999). Their distribution records across the country are also accumulated at the scale of 10×10 km in the national database of wildlife distribution (Ministry of the Environment of Japan 2002a).

Scope and outline of the thesis

There have been urgent needs for development of reliable techniques and schemes for biodiversity monitoring. 'Spatial ecological approach' explicitly considering ecological processes that are spatially dependent or operates across different spatial scales would provide effective tools to understand and predict the distribution, dynamics and immigration potential of target indicator species across landscape as mentioned above.

In the present thesis, dragonflies in agricultural and freshwater habitat complex as target species, I aim to answer the following questions to: (1) what factors do determine abundance and species richness at local habitat scale; (2)

what factors do determine the immigration potential of individuals at landscape scale and (3) what factors do determine the immigration potential of species to newly restored habitats. These questions would be fundamentally related to a general question, that is, how biodiversity can be monitored with 'dragonfly' as an indicator.

To answer these questions, I conducted field surveys at freshwater habitats, ponds that were simultaneously created by regional restoration projects in central Japan. In order to estimate the immigration potential of dragonflies, it is needed to observe the frequency of immigration to habitats of which initial condition has been known. A number of, or spatially larger aquatic habitats which were newly created in the projects have provided me good opportunities to examine the questions experimentally, or to validate model predictions at realistically larger spatial scale.

In the present chapter, I have reviewed the need for biodiversity monitoring and spatial ecological approach to the monitoring (Chapter 1).

Observed abundance of dragonflies at ponds might be influenced by local habitat characteristics as well as immigration potential of individuals. Therefore, before commenced to approach the landscape scale examination, I evaluated the effects of local pond characteristics on dragonfly abundance and species richness with a number of new ponds simultaneously created (Chapter 2).

In Chapter 3, I elucidated the effect of species characteristics and landscape factors on dragonfly abundance at the ponds, with statistically excluding the effects of local pond characteristics.

In chapter 4, I developed spatially explicit individual-based simulation

model to predict the immigration potential of individuals across landscape based on the patterns revealed in chapter 2 and 3.

In chapter 5, I proposed a technique to predict trajectory of species recovery based on the evaluation of the immigration potentials of individual species from a regional nested species pool, to a larger restored aquatic habitat in a wetland restoration project.

With these studies, I finally discussed the contribution of spatial ecological approach to development of techniques to predict the immigration potential of dragonflies and their distributions at larger spatial scales, and suggested that the approach would be sufficiently promising for biodiversity monitoring (Chapter 6).

Chapter 2 Dragonfly species richness on man-made ponds: effects of pond size and pond age on newly established assemblages

Introduction

One of the fundamental questions in community ecology is why some communities contain more species than others (Huston 1994). Species diversity can be determined by immigration, extinction or speciation, of which relative importance depends on spatial and temporal scales (Huston 1994). Since an assemblage of animals at a particular place is partly due to habitat selection by different species at ecological scale, we should reveal the importance of habitat selection, i.e., the processes by which animals choose places in which to live, as a factor which affects immigration or extinction rate of species (Morris 2003) and thus plays an important role in determining the community structures (Summerville *et al.* 2002). Furthermore, we should recognize that the habitat of a species varies with space and time.

With several reasons listed below, the immigration of dragonflies into newly created ponds provides a good opportunity to understand how habitat selection processes are responsible for the species richness and the assemblage patterns.

1) A large proportion of dragonfly species breed in lentic water: lakes, ponds, bogs, marshes (Silsby 2001), and paddies (Ueda 1998).
2) Many adult dragonfly species have high dispersal abilities (Corbet 1999) enough to immigrate to ponds soon after their creation.

3) Adult dragonfly species use aquatic vegetation as a cue of habitat selection (Corbet 1999; Gibson *et al.* 2004). In addition, some species use reflecting surface of water as a cue of habitat selection (Bernath *et al.* 2002; Corbet 1999).
4) Each species represents visible ecological features in their oviposition behaviors (exophytic vs endophytic) or manners of utilization of water area (flyer vs percher), which can influence habitat preference of the species in relation to aquatic vegetation or pond area. Fliers typically remain on the wing when active, whereas perchers, when mature, spend most of their time on a perch from which they make short flight (Corbet 1999). In the reproductive sites, flyer males may require larger habitat area in their territorial behavior.

Pond area has been reported to be an important factor determining species richness of various aquatic taxa, including fish (Koderic-Brown & Brown 1993), snails (Bronmark 1985; Lassen 1975), crustaceans (Fryer 1985), Diptera (Kholin & Nilsson 1998; Nilsson & Svensson 1995), and Odonata (Oertli *et al.* 2002).

In the adult dragonfly assemblages on newly created ponds, area dependency patterns of species richness can be simply emerged from the increase of total abundance in larger ponds, which includes the effects of sampling artifact or increasing of trapped individuals at larger ponds.

To discriminate the habitat selection processes from the abundance effects, I used a random placement model (Coleman *et al.* 1982) as a null model for the species-area relationship. Since habitat selection based on pond area can cause the nested structures of species distribution according to pond area,

nestedness of species distributional patterns was tested using a statistical method by Patterson and Atmar (1986).

Aquatic vegetations in ponds develop since their construction over time. Because adult dragonfly species use aquatic vegetation as a cue of habitat selection (Corbet 1999), species richness would depend indirectly on the pond age.

It is also to be clarified whether the change of species occurrence in relation to pond size and pond age reflects a dichotomy of dragonfly characteristics such as exophytic and endophytic ovipositors, or flyer and percher.

Study area

My study ponds were located at lowland area around Lake Kasumigaura (36°N, 140°E, about 2000 km^2 including Lake Kasumigaura) in Ibaraki Prefecture, Japan. In this area, more than 100 'dragonfly ponds' (Primack *et al.* 2000) were created during 1999– 2002 to promote the restoration of habitats for dragonflies and endangered aquatic plants, which was a part of activities of a public leading project for lake ecosystem restoration (Washitani 2003). These ponds created at similar times in the same region provide us a good experimental situation for studying ecological processes of the establishment of populations and assemblages of Odonata.

The ponds which we surveyed are located at northern part of the region (10 ponds) and south eastern part of the region (1 pond) that are separated about 30 km each other.

Methods

Pond characteristics

I surveyed 11 small shallow ponds built in 2001 except one which had been built in 2000 and was rebuilt in 2001 because of hard water leakage. All ponds were created or recreated in winter before dragonfly flying season. The size of the ponds varied from 29 to 144 m^2. These ponds were about 40 cm in depth and were sparsely fringed by aquatic plants such as *Nymphoides peltata*, *Sparganium erectum*, *Bolboschoenus fluviatilis*, and *Marsilea quadrifolia* that were introduced from nearby wetlands or abandoned paddies.

Dragonfly census method

I conducted periodic adult dragonfly censuses of these ponds during the period of adult dragonfly activity, from early May to early November, in 2001 and 2002, once or twice a month (7 times in 2001 and 9 times in 2002). Species richness (i.e., the total number of species present at the pond) and the population size of each species within the ponds (individual species abundance) were recorded. I censused adult dragonflies within whole area of the pond by walking along the pond's edge. Since the ponds were small enough, we could count all adult dragonfly individuals in the ponds. This took 2 to 11 minutes according to the pond size. As a rule, dragonflies were identified by sight, but we occasionally captured them using insect nets when it was not easy to identify them.

Vegetation census method

The percentage cover of vegetation in each pond was also recorded twice (late April and September) in 2001, and once every month in 2002.

Statistical analysis

A species – area relationship was calculated among sites and compared with a null model based on the random distribution of individuals among sites (Coleman *et al.* 1982). Under the random placement hypothesis, the number of species occurring at a particular pond is what one would expect if individuals were distributed at random among ponds and in proportion to the area of the pond. Furthermore, the probability of occurrence at a particular pond is assumed to be independent of the presence of other individuals. I calculated mean of predicted species richness over the ponds of these area using my adult dragonfly abundance data according to Coleman *et al.* (1982):

$$\bar{s}(\alpha) = S - \sum_{i=1}^{S} (1-\alpha)^{n_i}$$

where α was the area of each pond relative to the total area of ponds, S is the cumulative species richness of sites and n_i is the total abundance of i_{th} species. If the observed data do not significantly differ from the null distribution, the hypothesis of random placement cannot be rejected.

Communities have a "nested subset structure" if the species comprising depauperate communities are also found in progressively more species-rich sets (Patterson & Atmar 1986). I tested the statistical significance of the nested subset structure of the 11 adult dragonfly assemblages against the null hypothesis of

random assembly. For this purpose, I used the Monte Carlo simulation procedure of Patterson and Atmar (1986). The procedure of Patterson and Atmar (1986) counts the number of absences from perfect nestedness in a species-habitat matrix. A perfectly nested assemblage has a score = 0, and higher scores signify greater departures from perfect nestedness. I used their RANDOM1 routine which assumes that the species richness of the assemblage is the same as the observed values, and the probability of each species occurring in a assemblage is proportional to its actual frequency of occurrence among the ponds. In each case 10 000 simulations were run, and the number giving a degree of nestedness equal to, or greater than, that observed in the real assemblages gave a direct estimate of the probability under the null hypothesis.

Statistical analyses of relationships between assemblage patterns and environmental factors were conducted using StatView (SAS Institute Inc. Cary, NC, USA).

Results

I recorded a total of 1217 dragonflies of 20 species (7 zygopterans and 13 anisopterans) (Table 2-1) in 11 ponds during the study period from 2001 to 2002.

Effect of pond size on species richness

Species richness was significantly correlated with pond area in 2001 and 2002 (Figs. 2-1a, b).

To evaluate whether this association was simply a sampling

phenomenon due to larger habitats containing more individuals, the observed species-area relationship was compared to a null species-area model based on the random distribution of individuals across ponds (Coleman *et al.* 1982). The slope of observed species richness was significantly different from the random placement model ($P < 0.01$; t-test) such that small ponds tended to have fewer species than expected from the null model in 2001 (Fig. 2-1a). In 2002, the differences between the slopes were not significant ($P = 0.290$; t-test) (Fig. 2-1b).

The observed nestedness index (Patterson & Atmar 1986) for all Odonata species is 27 in 2001 and 28 in 2002 (Table 2-2), i.e., these faunas are far more nested than the species pool faunas produced by RANDOM1 models ($P <$ 0.05: 2001, $P < 0.005$: 2002; Monte Carlo simulation test). Nested patterns of species distribution have a relation to pond areas because species richness was significantly correlated with pond area.

Effect of pond age on species richness

Dragonfly species richness ($P < 0.05$; t-test) and summed abundance ($P < 0.05$; t-test) significantly increased with time since the pond was created (Figs. 2-2a, b). Vegetation coverage significantly increased during the study period ($P < 0.001$; t-test) from 2001 to 2002 (Fig. 2-3).

The changes of occupations of adult dragonfly species from 2001 to 2002 in the ponds were given in Table 2-2. Some species increased their occupation from 2001 to 2002. The oviposition types i.e., exophytic or endophytic, were also given in Table 2-1. The increase of occurrence of endophytic oviposition species except *Lestes temporalis* which oviposits on branches of tree

was not significantly larger than that of exophytic oviposition species ($P = 0.659$; t-test).

Discussion

Mechanisms for dependence of species richness on pond area

Species richness of adult dragonfly assemblages positively depended on pond area (Figs. 2-1).

In the random placement theory (Coleman *et al.* 1982), the probability of immigration of an individual into a pond was assumed to be linearly proportional to the pond's area. In 2001, the slope of the species-area curve was steeper than that predicted from the random placement model (Fig. 2-1a). On the other hand, the difference between the slopes was not clear in 2002 (Fig. 2-1b). In 2001, the species richness observed were lower than that expected from random placement especially in smaller ponds. This indicates that the responses of individuals to pond areas were not always linear. The deviation may be partly because some species avoid small ponds and others do not.

In 2002, the increase in species which favor well vegetated ponds but do not markedly respond to the pond area was likely to counteract the effect of the habitat selection according to pond area.

The nestedness pattern associated with the habitat size can be emerged if individual species have the minimum habitat size thresholds to keep viable population (e.g., Koderic-Brown & Brown 1993; Worthen *et al.* 1998), which vary according to the species, and determined by the dispersal or colonizing ability within a site of species, coupled with a range of site areas (Cook & Quinn

1995; Loo *et al.* 2002) or by sampling artifact (Cutler 1994). In addition, at an ecological fine spatial scale, the habitat selection of individuals based on habitat size can cause the nestedness (Summerville *et al.* 2002).

In the present study, the assemblages were significantly nested (Table 2-2), and the nestedness pattern was related to pond area as shown in many studies (e.g., Berglund & Jonsson 2003; Hecnar *et al.* 2002). Therefore the mechanism which caused the nested distribution of adult dragonfly species was likely to be responsible for the area dependent patterns of their species richness.

Dragonfly species can be categorized into two groups according to the way by which they use the water area, i.e., percher or flyer (Corbet 1999). Whereas the perchers usually perch on aquatic vegetation in ponds, the fliers keep on flying above water area.

In the present study, *Pantala flavescenfs, Pseudothemis zonata, Anax parthenope julius*, *Anax nigrofasciatus nigrofasciatus* and *Anotogaster sieboldii* were fliers, and were not observed at small ponds (tenth or eleventh rank order of pond area) during two years. *Pseudothemis zonata* and *Anax parthenope julius* of which males have territories on the open water areas were only observed at large ponds (first through fifth rank order of pond area) during two years. Since flyer species were not observed at small ponds, the nestedness patterns observed in the present study can be partly ascribed to their preference to the larger ponds.

Effects of vegetation development on species diversity

The species richness significantly increased with pond age (Fig. 2-2a). This pattern may reflect the habitat selection by adult dragonflies using the aquatic

vegetation as a cue because the increase of species richness was correlated with the development of aquatic vegetation (Figs. 2-2a, 2-3). This interpretation may be supported by the increases in the occurrence of some endophytic oviposition species from 2001 to 2002 (Table 2-1). However, the possibility of age dependency due to other mechanisms such as the emergences of some species carried over from 2001 in ponds increased the species richness of ponds in 2002 was not rejected because exophytic ovipositing species, such as *Crocothemis servilia mariannae, Sympetrum kunckeli* and *Orthetrum triangulate melania* also increased their occurrence from 2001 to 2002 (Table 2-1).

Although *Crocothemis servilia marianna*, *Sympetrum kunckeli* or *Orthetrum triangulate melania* were exophytic ovipositing species, they use aquatic vegetation to perch. In addition, the larvae of *Crocothemis servilia marianna* and *Sympetrum kunckeli* inhabit clinging to stems of emergent ponds in ponds. These facts are likely to indicate that the oviposition traits were not always enough to explain the species' preference to aquatic vegetation, and other factors such as manners of utilization of water area or characteristics of larval habitats are important in some species.

In summary, the species richness of adult dragonflies in small man-made ponds was influenced by the pond area and the pond age. These area and age dependent patterns were explained by species nestedness and vegetation development, in which habitat selection by adult dragonfly species might be a major underlying mechanism.

Table 2-1. Observed species in two study years, change in species occurence across ponds from 2001 (a) to 2002 (b) and their type of oviposition.

	Species name	Number of ponds where the species presented			Endophytic species
		a	b	b - a	
1	*Crocothemis servilia mariannae*	4	9	5	
2	*Cercion sieboldi*	1	5	4	●
3	*Anax nigrofasciatus nigrofasciatus*	1	5	4	●
4	*Pantala flavescens*	1	5	4	
5	*Indolestes peregrinus*	0	4	4	●
6	*Ischnura senegalensis*	6	9	3	●
7	*Anotogaster sieboldii*	1	4	3	
8	*Sympetrum kunckeli*	1	4	3	
9	*Orthetrum triangulate melania*	0	3	3	
10	*Ischnura asiatica*	9	11	2	●
11	*Sympetrum frequens*	10	11	1	
12	*Orthetrum albistylum speciosum*	9	10	1	
13	*Anax parthenope julius*	1	2	1	●
14	*Sympetrum infuscatum*	11	11	0	
15	*Pseudothemis zonata*	1	1	0	
16	*Sympetrum darwinianum*	5	4	-1	
17	*Ceriagrion melanurum*	1	0	-1	●
18	*Lestes sponsa*	1	0	-1	●
19	*Sympetrum eroticum eroticum*	2	0	-2	
20	*Lestes temporalis*	10	4	-6	*

Footnote: *Lestes temporalis* is endophytic ovipsotion species but oviposits into branches of tree.

Table 2-2. Occurrence patterns of dragonfly species in ponds in 2001and 2002. Species are ranked by the frequency of sites occupied, and sites are ranked by richness. + represents deviation from perfect nestedness. The sum of the number of deviations is the Patterson and Atmar (1986) nestedness statistic, N, which is compared with scores generated by their RNDOM1 program (see text). Species are significantly nested in 2001 ($P < 0.05$) and 2002 ($P < 0.005$). * represents flyers and (*) represents a lotic flyer, i.e., *Anotogaster sieboldii*.

Rank order of pond area	Species (2001)																		Species richness
	14	20	11	10	12	6	16	1	19	17	7	13	4	15	18	3	2	8	
2	O	O	O	O	O	O	O	O	O	O	O	+	+	+	+	+	+	+	11
3	O	O	O	O	O	O	O	O	+				O		+	+	+	+	9
5	O	O	O	O	O	+	O	O	+			O		O	+	+	+	+	9
1	O	O	O	O	O	O	+		O						O		+	+	8
4	O	O	O	O	O	+	O	O								O	+	+	8
8	O	O	O	O	O	O	O												7
7	O	O	O	O	O	+											O	O	7
6	O	O	O	O	O	O													6
9	O	O	+	O	+	O													4
10	O	O	O																3
11	O		O		O														3
Species occurrence	11	10	10	9	9	6	5	4	2	1	1(*)	1*	1*	1*	1	1*	1	1	

Rank order of pond area	Species (2002)																	Species richness
	10	11	14	12	1	6	2	3	4	20	16	8	5	7	9	13	15	
4	O	O	O	O	O	O	O	O	+	O	O	O	+	O	O	+		13
1	O	O	O	O	O	O	O	+	O	O	O	+	O	+	+	O	O	13
9	O	O	O	O	O	O	+	O	+	O	+	O	O	O	O	+		12
7	O	O	O	O	O	O	O	O	+	O	O	+	+	+	+	+		10
2	O	O	O	O	O	O	+	O	O		+	O	O	+	+	+		10
8	O	O	O	O	O	O	O		O					O				9
3	O	O	O	O	O	O	+		O			O	O	+				9
5	O	O	O	O	O	+	+	O	+		O			+	O	O		9
6	O	O	O	O		O			O					O				7
10	O	O	O	O	O	O	O											7
11	O	O	O															3
Species occurrence	11	11	11	10	9	9	5	5*	5*	4	4	4	4	4(*)	3	2*	1*	

Footnote: Each species number corresponds to that given in Table 2-1.

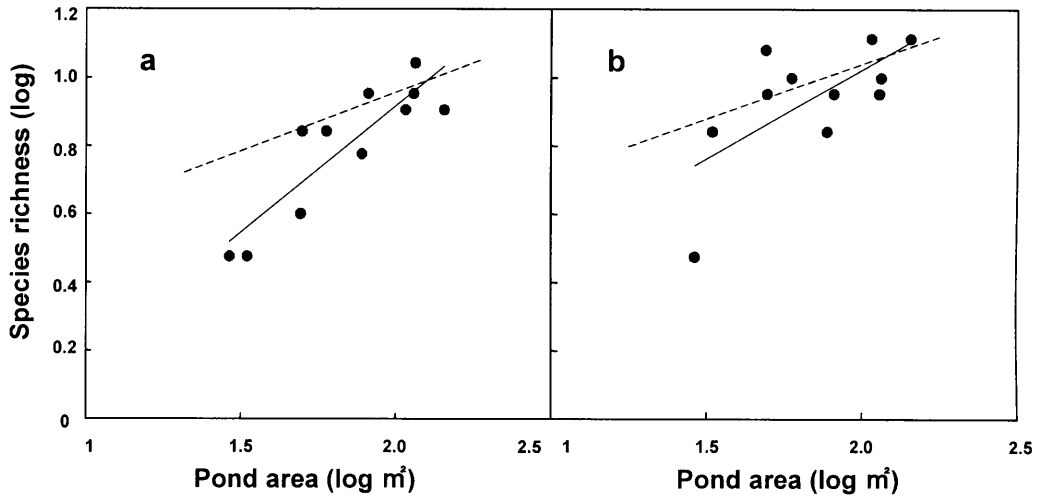


Figure 2-1. Relationships between pond area and observed and expected species richness in 2001 (a) and 2002 (b) of the dragonfly assemblages in the ponds. The solid lines represent observed species- area relationships and the broken lines represent expected species-area relationships. Expected values were obtained from a null model based on random placement of individuals across ponds. Slopes are significantly different ($P < 0.01$) in 2001 (a) and not significant ($P = 0.290$) in 2002 (b).

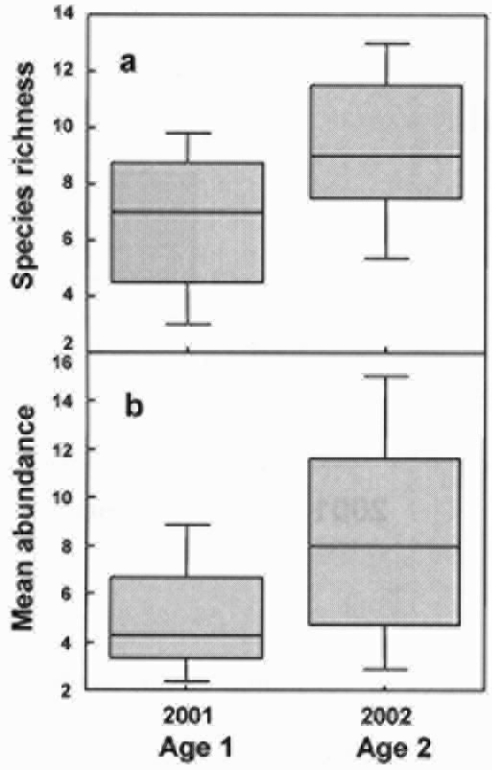


Figure 2-2. Temporal changes of species richness (a) and mean abundance (per observation) (b). Medians (horizontal bars in boxes), quartiles (boxes), and 10th and 90th percentile values (vertical bars protruding from boxes) are presented. Increases from 2001 to 2002 were significant in both species richness ($P < 0.05$) and mean abundance ($P < 0.05$).

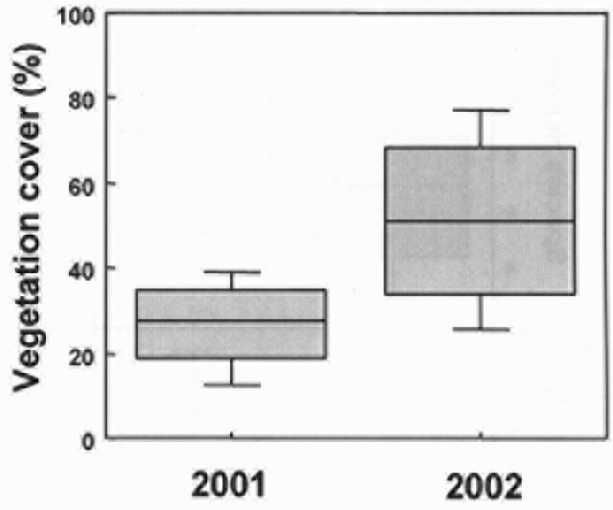


Figure 2-3. Temporal changes of vegetation cover. Medians (horizontal bars in boxes), quartiles (boxes), and 10th and 90th percentile values (vertical bars protruding from boxes) are presented. Increases from 2001 to 2002 were significant ($P < 0.001$).

Chapter 3 Differential abundance sensitivity to landscape structure between life-history groups of dragonflies

Introduction

Habitat destruction and fragmentation are the most important causes of the increase in the rate of species extinctions in recent decades (Fahrig 2003). Nevertheless, mounting empirical evidence suggests that not all species decline towards extinction following habitat fragmentation, and some species are more robust than others against fragmented landscapes (e.g., Driscoll & Weir 2005; Purtauf *et al.* 2005). This may be partly because each individual taxon responds differently to the spatial patterns or dynamics of its environment. However, if it is correct that species sharing similar traits (i.e., functional groups) respond similarly to changes in the spatial environment, we can reduce the great diversity of plant and animal species to fewer operational entities (i.e., functional groups) for the purpose of the predicting their response to environmental changes such as habitat fragmentation.

Several population or ecological features have been hypothesized to explain the sensitivity of species to habitat fragmentation (Ewers & Didham 2006; Henle *et al.* 2004). However, although the life cycles of many animals have discrete stages, such as larval, juvenile, and adult stages, that depend on different habitats (i.e., complex life cycles senseu Wilbur 1980), only a few studies have examined how these spatially explicit population stage structures (i.e., when different life stages live in different locations) may affect population size and

dynamics, and thus the sensitivity to habitat fragmentation (Andren *et al.* 1997; Pope *et al.* 2000). In a recent paper, Halpern *et al.* (2005) predicted that the average life span of a species partially explains the types of habitat (i.e., adult vs. juvenile habitat) that are likely to limit the abundance of species. That is, species with a longer adult stage are more likely to be limited by the availability of adult habitat unless the juvenile habitat is extremely limited. In contrast, species with a shorter adult stage may be rather more limited by the availability of juvenile habitat. This suggests that the relative duration of individual life stages may be an important predictor for the sensitivity of animals with complex life cycles to habitat destruction and fragmentation.

Dragonflies (Odonata) are common invertebrates in various aquatic ecosystems. They have complex life cycles, shifting from aquatic to terrestrial habitats in their adult stage, thus crossing ecosystem boundaries (Knight *et al.* 2005). Their adult life stage consists of three successive phases: the pre-reproductive, reproductive, and putative post-reproductive phases (Corbet 1999). During their pre-reproductive phase, individuals are compelled to move between two types of habitats, from aquatic areas to terrestrial areas and back again. Woodlands or forests, in which conditions such as temperature and humidity are relatively moderate, provide dragonflies with suitable terrestrial habitats (Corbet 1999). Pre-reproductive phase dragonflies of many species use these habitats for foraging, resting, and avoiding unsuitable (dry or hot) conditions (Fincke 1992; Morton 1977; Watanabe *et al.* 2005). Among species, the duration of the pre-reproductive phase varies from a few days to several months (Corbet 1999).

Because a longer pre-reproductive phase is dependent on the availability of terrestrial habitats in the landscape, I assumed that the duration of each life stage, especially the duration of the pre-reproductive phase, is a major factor determining the sensitivity of dragonflies to fragmentation of terrestrial habitats. To verify the importance of this hypothesis, an important prerequisite is the identification of the relationships between the duration of the pre-reproductive phase and the species' sensitivity to changes in the landscape structure. The main objective of the present chapter was to examine whether species that have a longer pre-reproductive phase are more sensitive to landscape structure than those with a shorter pre-reproductive phase. To test this hypothesis, I first conducted periodic censuses of adult dragonflies at small, newly created man-made ponds. I then compared the two functional groups having pre-reproductive phases of different duration (i.e., long-phase vs. short-phase species) in terms of the degree to which species abundance depended on the landscape structure (i.e., woodland around the sampling ponds).

Methods

Classification of life history of pond-breeding dragonflies

Contrasting life-history strategies of dragonflies in the temperate region are recognized based on the duration of the adult pre-reproductive phase: some species have a long pre-reproductive phase of more than 1 month after which they return to aquatic habitats to reproduce, whereas other species have a short pre-reproductive phase of less than 10 days (Corbet 1999). The long-phase species spend a much longer time in terrestrial habitats such as woodlands, forests,

and grasslands before returning to aquatic habitats (Watanabe *et al.* 2004; Watanabe & Taguchi 1988). In Japan, species belonging to the genera *Sympetrum* and *Lestes* are representative long-phase species (e.g., Corbet 1999; Sugimura *et al.* 1999; Taguchi 1987). Species such as *Indolestes peregrinus* that overwinter in the adult stage have an exceptionally long pre-reproductive phase (ca. 9 months). In contrast, species of the genus *Ischnura* are reported to have a short pre-reproductive phase (from 1 to 5 days; Corbet 1999). Although the precise duration of their pre-reproductive phase has not been reported, spring ephemerals such as *Anax nigrofasciatus nigrofasciatus* (Sugimura *et al.* 1999) or colonizer species which have 'fast' life cycles and are multivoltine such as *Orthetrum albistylum speciosum* and *Pantala flavescens* (Sugimura *et al.* 1999) apparently have a shorter pre-reproductive phase.

Study site

I surveyed 48 small shallow ponds that were newly created between 1999 and 2003 around Lake Kasumigaura (lat 36°N, long 140°E) in Ibaraki Prefecture, eastern Japan (median distance between the nearest ponds: 4805 m; Fig. 3-1). These ponds were created to promote the restoration of habitats for dragonflies and endangered aquatic plants in wetland restoration activities shared by local NGOs and schools (Washitani 2003). The surface areas of the ponds vary from 13 to 144 m^2. The ponds have maximum depths of about 40 cm, have gently sloped borders, and are sparsely fringed by aquatic plants such as *Nymphoides peltata* (Gmel.) O. Kuntze, *Sparganium erectum* L., *Bolboschoenus fluviatilis* (Torr.) A. Gray, and *Marsilea quadrifolia* L. that were introduced from nearby wetlands or

abandoned paddies. The ponds are supplied with water as the need arises to prevent them from drying.

Species abundance data

I conducted periodic censuses of adult dragonflies at each of the 48 ponds during the season of adult dragonfly activity in 2003. To cover all phenological groups (from spring species to late summer and autumn species), we did a census of each pond once in each of three time periods: May 15 to June 3, July 27 to August 7, and September 29 to October 9. Abundance data were collected by the same method as in chapter 2. The abundance data from each census was pooled for each species for each sampling pond, and the abundance data for all species was log-transformed using the formula $\log_{10}(x + 1)$. Abundance of each species was standardized to have a mean of 0. Species were classified as either long- or short-phase species and treated separately in the following analysis.

Explanatory variables

Sampling pond characteristics. In a previous study (Kadoya *et al.* 2004; Chapter 2), I demonstrated that pond surface area and vegetation cover played an important role in determining the species composition of adult dragonflies at the sampling ponds. Therefore, I included these two pond characteristics as explanatory variables in the statistical models. Vegetation cover (including any type of aquatic plants) was recorded using 10% increments during each census period. The variables were standardized to have a mean of 0 and a standard deviation of 1.

Landscape metrics. I selected three landscape variables to model the species abundance of dragonflies at the sampling ponds: the presence of irrigation ponds or other small reservoirs, deciduous forests, and evergreen forests in the area around the sampling ponds. Irrigation ponds are likely to be the primary habitats for larvae of the dragonflies in the study region, whereas deciduous and evergreen forests would provide summer or winter habitats for adults. The distribution of irrigation ponds was determined from a 1:25 000 scale digital topographic map (Geographical Survey Institute of Japan), and the distributions of deciduous and evergreen forests were obtained from 1:50 000 scale national land-cover data (sites sampled around 1998; Environment Agency of Japan). These variables were mapped spatially as raster grid layers with a 25 × 25 m cell size using ESRI ArcGIS 9.0 software (Environmental System Research Institute, Redlands, CA, USA). Each cell in each layer was assigned a value of 1 or 0 according to the presence or absence of a variable.

For each variable and for each sampling pond I calculated a set of distance-weighted metrics (Rhodes *et al.* 2006). These metrics are the weighted means of the values of the variables around each sampling pond, with an exponential decline in weighting with distance from the sampling pond. For sampling pond $i = 1, \ldots, M$, the metric X_i is calculated as

$$X_i = \frac{\sum_{c=1}^{k} V_c \exp(-\lambda d_{ic})}{\sum_{c=1}^{k} \exp(-\lambda d_{ic})} \quad (1)$$

where V_c is the value of the variable in cell c; d_{ic} is the distance between sampling

pond i and the centre of cell c; λ is the scale parameter for the negative-exponential function; and the sum is over all cells in the landscape, $c = 1,\ldots, k$. I considered all cells within the range of 30 km from the nearest sampling pond. All metrics were standardized to have a mean of 0 and a standard deviation of 1.

The parameter λ controls how rapidly the influence (i.e., weighting) of the variable declines with distance. If λ is small, then there is a slow decline in weighting with distance and values of the variable close to and far from each sampling pond determine the value of the metric. The pattern of dragonfly dispersal has been well explained by a negative-exponential function (Conrad *et al.* 1999); however, the distances over which they travel vary from several dozen metres to several kilometres according to species or the type of landscape (e.g., Conrad *et al.* 1999; Corbet 1999; Knaus & Wildermuth 2002; Purse *et al.* 2003; Watanabe *et al.* 2004; Watanabe & Taguchi 1988). Therefore, I employed an exploratory approach and considered 30 different values of λ, corresponding to negative-exponential probability distributions with expected values equal to mean dispersal distances from 100 to 3000 m at 100-m intervals (i.e., 30 spatial scales for each metric). The λ values we used were from 10.0×10^{-3} per metre for an expected value of 100 m to 0.3×10^{-3} per metre for an expected value of 3000 m.

Spatial data. The spatial dataset consisted of nine spatial variables calculated from the geographic coordinates of each sampling point using the following procedure. The x- and y-coordinates (x: longitude, y: latitude) of the sampling points were centred on their means, and the following synthetic variables were

calculated: x, y, xy, x^2, y^2, x^3, y^3, x^2y, and xy^2. Each variable was then standardized by dividing it by its standard deviation (Trend Surface Analysis: Borcard et al. 1992; Legendre 1993).

Statistical modelling

I used redundancy analysis (RDA) to model the vectors of relative abundance of long- and short-phase dragonfly species (hereafter species abundance). RDA can be viewed as the canonical extension of principal component analysis (PCA), with the ordination vectors being constrained by multiple regression to be linear combinations of the original explanatory variables (Legendre & Legendre 1998).

To check for spatial autocorrelation in the species abundance data of each group, the spatial data were regressed against the species abundance data using RDA. To reduce the number of spatial variables, I first performed forward stepwise selection based on Akaike's information criterion (AIC). To remove the effects of spatial autocorrelation in the following analyses, these selected variables were always considered as covariables.

To reduce the number of possible combinations of explanatory variables to a manageable level, I chose only one of the 30 spatial scales calculated for each metric. The spatial scale chosen was that which yielded the lowest AIC from the univariate models. In the univariate models, the spatial variables chosen above were included as covariables.

I constructed a set of candidate models to examine our hypothesis that the sensitivity to landscape structure would be stronger in long-phase species than in short-phase species. In all candidate models, the characteristics of the sampling

ponds (i.e., pond surface area and vegetation cover) were included *a priori* based on the results of Kadoya *et al.* (2004). I categorized irrigation ponds as an aquatic landscape metric, and I categorized deciduous and evergreen forests as terrestrial landscape metrics. I then included the combinations of landscape metrics sets (i.e., + none, + aquatic, + terrestrial, + both). Therefore, I constructed four candidate models for each species group. I then ranked these models by their AIC values and calculated the Akaike weight of each model. The Akaike weight of a model is the relative likelihood of the model to accurately reflect reality compared with all other models in the set (Burnham & Anderson 2002).

To interpret the species responses to major environmental gradients, I produced correlation biplots (Legendre & Legendre 1998) of the most parsimonious models for the long- and short-phase species groups. The correlation biplots illustrate the relationships between the species, environmental variables, and ordination axes derived from the species abundance data. The angles between variables in the biplot reflect their correlations (Legendre & Legendre 1998).

Relative effects of space versus environment

To compare the relative effect of space (geographic coordinates) versus environmental factors (local and landscape metrics) on the species abundance of each group, I conducted a variance decomposition analysis (Borcard et al. 1992) using the variable set that produced the most parsimonious model in the previous model selection procedure. In the analysis, the variance of the species abundance data for each species group was decomposed into the purely spatial component,

purely environmental component, and spatially structured environmental component (Borcard et al. 1992) using partial RDA.

I used R release 2.2.1 (package 'vegan') to conduct these analyses (R Project for Statistical Computing, http://www.r-project.org/).

Results

Observed species

I recorded a total of 1094 dragonflies belonging to 18 species (6 zygopterans and 12 anisopterans) at the 48 ponds (Table 3-1). I excluded tenerals (individuals with a nearly colourless, unhardened integument and with weak and fluttering flight; Corbet 1999) because they were apparently recorded immediately after emergence and had not yet interacted with habitats beyond their natal ponds. Species that occurred at fewer than six ponds were excluded from the statistical analyses because I used a maximum of five variables (i.e., two sampling pond variables and three landscape metrics) in the model selection procedure. Accordingly, I analyzed the abundance patterns of 923 individuals belonging to 10 species consisting of 5 long- and 5 short-phase species (Table 3-1).

Model selection

From the forward selection of spatial variables based on AIC, we selected two terms from the spatial data set, x^3 and y, for long-phase species; however, for the short-phase species, no variables produced a more parsimonious model than the null model. Therefore, we included x^3 and y as covariables in the following model selection procedure for long-phase species, but none for short-phase species.

Based on AIC of the univariate models, irrigation ponds scaled to 1400 m (POND1400); (i.e., the pond metric calculated using the value of λ corresponding to negative-exponential probability distributions with expected values equal to 1400 m), deciduous forests scaled to 600 m (DF600), and evergreen forests scaled to 3000 m (EF3000) were selected as landscape metrics for long-phase species, while irrigation ponds scaled to 200 m (POND200), deciduous forests scaled to 100 m (DF100), and evergreen forests scaled to 200 m (EF200) were selected for short-phase species (Table 3-2).

In the model selection procedure, the most parsimonious model for the long-phase species (AIC = –61.32) contained the sampling pond variables (i.e., pond surface area and vegetation cover) and the terrestrial landscape metrics (i.e., DF600 and EF3000; Table 3-2). For short-phase species, the linear combination of sampling pond variables and aquatic landscape metrics (i.e., POND200) produced the most parsimonious model (AIC = –52.87; Table 3-2).

As shown in the correlation biplots of the most parsimonious models for the long- and short-phase species (Fig. 3-2), the abundance of most species was positively related to the surface area of the sampling ponds. In addition, the abundances of *Sympetrum kunckeli* (long-phase), *Sympetrum darwinianum* (long-phase), *Ischnura asiatica* (short-phase), and *Anax nigrofasciatus nigrofasciatus* (short-phase) were positively related to the vegetation cover of the sampling ponds. The abundances of the five long-phase species were all positively related to forest metrics to greater or lesser degrees. In particular, the abundance of *I. peregrinus* was closely related to the metric of deciduous forest scaled to 600 m.

Effects of spatial autocorrelation

The results of the variance decomposition (Fig. 3-3) show that the two terms from the spatial dataset, x^3 and y, explained 13.5% of the variance in long-phase species abundance, independent of environmental variables (pond surface area, vegetation cover, DF600, and EF3000). For the short-phase species, however, no spatial terms were selected and 31.0% of the variance was explained by environmental variables (pond surface area, vegetation cover, and POND200).

Discussion

Sensitivity to landscape structure

Previous studies have indicated that even within the same landscape, the response to the landscape structure can differ in direction or spatial scale from species to species (e.g., weak-flying insects: Krawchuk & Taylor 2003; amphibians: Van Buskirk 2005). Our results demonstrated that, for dragonflies, the sensitivity to landscape structure could be partially predicted from the life-cycle type categorized by the duration of the pre-reproductive phase. This suggests that the duration of each life stage should be considered as essential when determining which type of habitat is most likely to limit the abundance of species (e.g., aquatic vs. terrestrial habitats for dragonflies).

The most parsimonious models indicated that forest habitats were a major determinant for long-phase species, which stay for a longer time in terrestrial habitats, whereas short-phase species respond more sensitively to aquatic habitats (i.e., irrigation ponds). Although the relative likelihood of the

most parsimonious model (i.e., the Akaike weight) for each species group was not much higher than that of the next most parsimonious model, especially for short-phase species, the correlation between species abundance and the environmental variables included in the most parsimonious model did not contradict the ecological and behavioural characteristics known for this species group. For most species, abundance was positively related to pond surface area, as demonstrated in a previous study (Kadoya *et al.* 2004; Chapter 2), and for species such as *I. asiatica* and *A. nigrofasciatus nigrofasciatus* that depend on vegetation for oviposition or territorial behaviour, abundance was positively related to vegetation cover. In addition, and most importantly, the abundance of each of the five long-phase species was positively related to forests, their summer or winter habitats. These results support our hypothesis that sensitivity to landscape structure would be stronger in the species with a longer pre-reproductive phase than the short-phase species.

Among the long-phase species, the abundance of *I. peregrinus* was more strongly related to the metric of deciduous forests scaled to 600 m than were the abundances of the *Sympetrum* species, which were more closely related to the metric of evergreen forests scaled to 3000 m. The differences in response scales within the long-phase group may be ascribed to differences in their flight abilities. Assuming that body size is an indicator of dispersal ability (Bowman et al. 2002; Holland et al. 2005; Sutherland et al. 2000), *I. peregrinus* with its shorter wing length (19-22 mm; Sugimura et al. 1999) would be a weaker flier than the *Sympetrum* species with their longer wing lengths (*S. darwinianum*: 25–31 mm, *S. kunckeli*: 20–27 mm, *S. infuscatum*: 25–37 mm; Sugimura *et al.*, 1999). Because *I.*

peregrinus overwinters during the adult pre-reproductive phase, *I. peregrinus* moving during this phase would be more vulnerable to early season low temperatures than would *Sympetrum* species.

Spatial scale of the sensitivity

The results of the model selection demonstrated that the duration of the pre-reproductive phase was also related to the spatial scale of the landscape metrics on which the species depend, i.e., the scales of selected landscape metrics were larger in long-phase species than in short-phase species. This was probably because long-phase species have more opportunity to interact with habitats in the landscape and thus interact over potentially broader spatial scales. These results suggest that the life-history characteristics of dragonflies could be related not only to their sensitivity to landscape structure, but also to functional connectivity, the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993).

Interpretation of spatial autocorrelation

Spatial autocorrelation of species distribution could be caused by spatially structured environmental factors such as landscape structure and climate or by biological processes such as dispersal and biological interaction (Legendre 1993). Therefore, the scale and magnitude of spatial autocorrelation would strongly depend on the geographical and biological conditions in each study system. Nevertheless, interpretation of spatial autocorrelation patterns may give some information on the mechanisms that determine species distribution (Legendre

1993). In the present study, the abundance of long-phase species had an apparently larger spatial component of variance. The likely reasons for the higher spatial autocorrelation are (1) the effects of unmeasured, spatially structured landscape structures or (2) the effects of movements of individuals among sampling ponds. The effects of other unmeasured, spatially structured variables such as climate or disease would be minor or negligible because these factors are likely to affect both long- and short-phase species simultaneously. Although the composite effects of landscape structure and movements on the observed autocorrelation pattern cannot be distinguished in a strict sense, I speculated that unmeasured, spatially structured landscape effects were dominant because the trend surface of species abundance across sampling ponds modelled by spatial variables (i.e., x^3 and y) seemed to be related to the distribution of forests at a larger scale. It is possible that ponds closer to one another had a similar 'background' with regards to the amount of forests surrounding them because of the spatial trend of forest distribution in the studied landscape, and thus the abundance patterns of long-phase species would become more similar among closer ponds. In that case, our hypothesis that the sensitivity to landscape structure would be stronger in long-phase species than in short-phase species would be supported more strongly.

Table 3-1. Observed dragonfly species, the number of ponds at which they were recorded, and their life-history group based on the duration of the pre-reproductive phase (short: < 10 days = short-phase; long: > 1 month = long-phase). Ten species with abbreviation were analyzed.

Species	Abbreviation	Duration of pre-reproductive phase	No. of ponds
Sympetrum frequens	*fre*	Long	41
Sympetrum infuscatum	*inf*	Long	40
Sympetrum kunckeli	*kun*	Long	23
Indolestes peregrinus	*per*	Long	12
Sympetrum darwinianum	*dar*	Long	11
Lestes temporalis	-	Long	5
Sympetrum eroticum eroticum	-	Long	3
Lestes sponsa	-	Long	1
Ischnura asiatica	*asi*	Short	43
Orthetrum albistylum speciosum	*alb*	Short	33
Crocothemis servilia mariannae	*ser*	Short	22
Ischnura senegalensis	*sen*	Short	17
Anax nigrofasciatus nigrofasciatus	*nig*	Short	12
Cercion sieboldi	-	Short	5
Pantala flavescens	-	Short	3
Anax parthenope julius	-	Short	2
Orthetrum triangulate melania	-	Short	1
Pseudothemis zonata	-	Short	1

Table 3-2. Model ranking, Akaike's information criteria (AIC), Akaike weights (*w*), and selected variables used to construct models. The Akaike weight of a model is the relative likelihood of the model compared with all other models in the set (Burnham & Anderson 2002).

Model ranking	AIC	ΔAIC	w	Candidate model	Selected variable
(a) Long-phase species					
1	-61.32	0.00	0.39	Local + Land_f + Cov.	Local: AREA, VEG
2	-60.67	0.65	0.28	Local + Cov.	Land_p: POND1400
3	-59.79	1.53	0.18	Local + Land_p + Land_f + Cov.	Land_f: DF600, EF3000
4	-59.45	1.87	0.15	Local + Land_p + Cov.	Covariable: x^3, y
(b) Short-phase species					
1	-52.87	0.00	0.31	Local + Land_p	Local: AREA, VEG
2	-52.78	0.09	0.30	Local	Land_p: POND200
3	-52.27	0.60	0.23	Local + Land_p + Land_f	Land_f: DF100, EF200
4	-51.64	1.23	0.17	Local + Land_f	Covariable: none

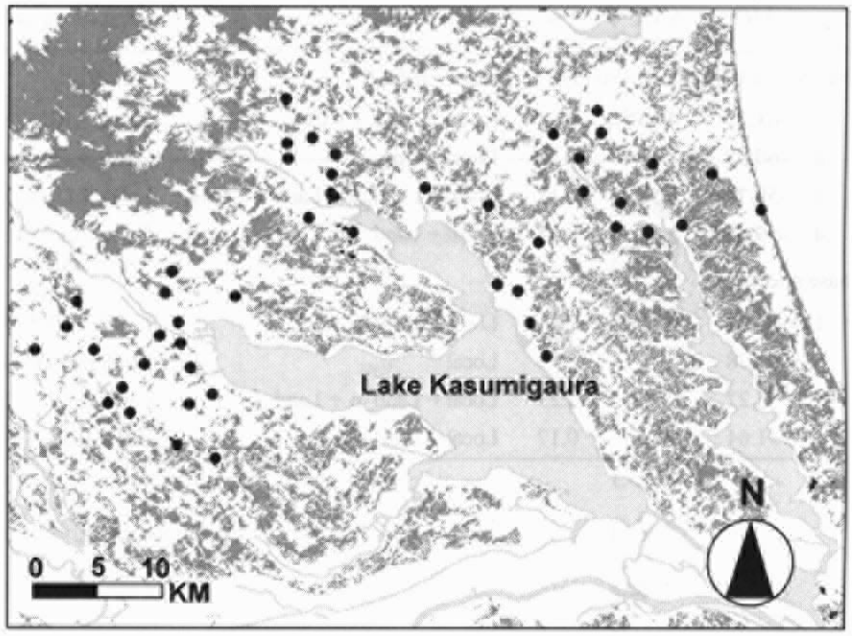


Figure 3-1. The study site in Ibaraki Prefecture (lat 36°N, long 140°E), eastern Japan. Solid circles represent sampling ponds, and dark grey patches represent the distribution of deciduous and evergreen forests.

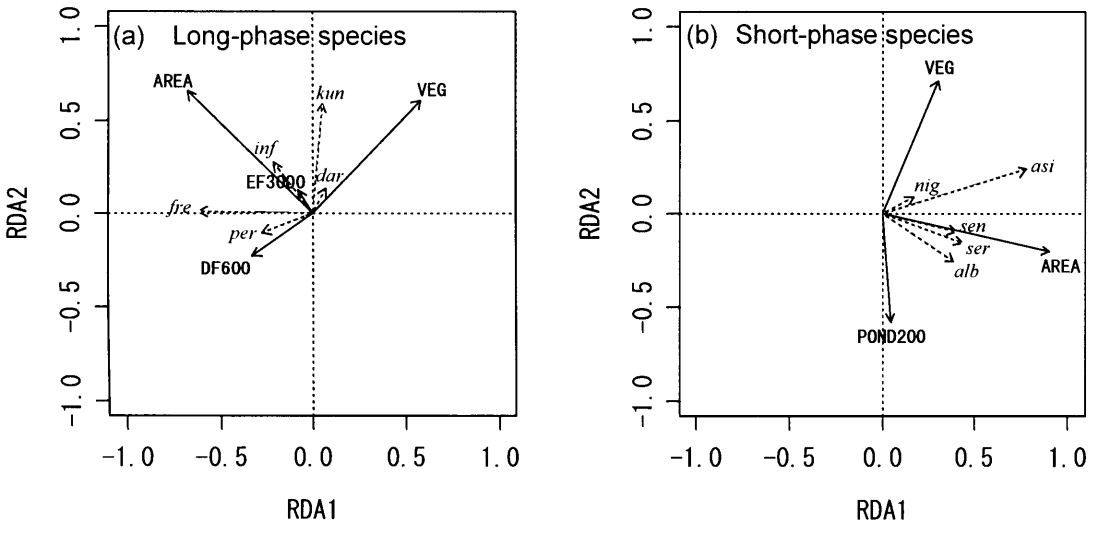
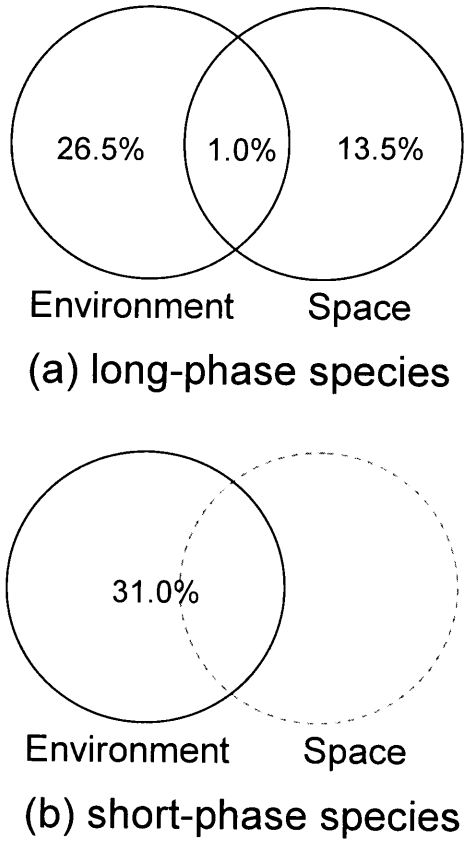


Figure 3-2. Correlation biplots (Legendre & Legendre 1998) obtained from redundancy analyses (RDA) of (a) long-phase and (b) short-phase dragonfly species. Species and environmental variables are indicated by arrows. Species names are abbreviated as in Table 3-1. The angles between the species arrows, the environmental variables, and the ordination axes in the biplots reflect their correlations (Legendre & Legendre 1998). If the arrow for an environmental variable points in a similar direction to a species arrow, the environmental and species values are positively correlated. Spatial data (x^3, y) were used as covariables in the analysis of long-phase species. No covariables were included in the analysis of short-phase species.



Figures 3-3. Percent of total variance in the species abundance of (a) long-phase and (b) short-phase dragonfly species explained by environmental variables, spatial variables, and both environment and space together. The variables used with the most parsimonious models in Table 3-2 were used here. Of the total variation in the (a) long-phase and (b) short-phase species, 59% and 69% were left unexplained, respectively.

Chapter 4 Landscape-scale prediction of the potential of immigration of dragonfly to newly created breeding habitats

Introduction

In the developed regions where natural habitats have been severely fragmented by intensive farming and/or urbanization, biodiversity conservation is a growing issue in landscape planning and ecosystem management. The habitat fragmentation limits the movement of individuals among resource patches and can be an important determinant of persistence, size, and genetic diversity of a population. Thus, there is great interest among ecologists in measuring connectivity, defined as "the degree to which the landscape facilitates or impedes movement of organisms among resource patches" (Taylor *et al.* 1993). Although the term connectivity is used primarily to describe a property of the landscape (i.e., landscape connectivity), the term can be also defined, from a patch-based point of view, as the probability r_{ij} of a certain patch j being reached by an emigrant from a certain patch i (i.e., patch connectivity) (Moilanen & Hanski 2001; Tischendorf & Fahrig 2000, 2001).

In the ecological literature, indices based primarily on habitat structure are often used as a surrogate for patch connectivity. The easiest approach is to take the distances between patches into account (Moilanen & Nieminen 2002). In the literature, this is normally done by describing r_{ij} as a function of distance between start and target patch. One of the simplest and most obvious approaches to describing this relationship is the exponential form, where r_{ij} declines

exponentially with distance (Hanski 1994). Although this exponential dispersal function is valid for a variety of small, passively moving organisms, it is debatable whether this approach is suitable to describe more complex situations, especially when the individuals' dispersal behavior should be taken into account (Bender & Fahrig 2005; Winfree *et al.* 2005). Describing the patch connectivity can also become complex in a situation where the animals have complex life cycles (Wilbur 1980) and change their habitat types ontogenetically (Chapter 3).

The loss of semi-natural habitats due to agricultural intensification and marginalization of traditional agricultural systems, both of which have led to the abandonment of traditional land uses, is one of the main threats to biodiversity in agricultural ecosystems (Krebs *et al.* 1999; Ormerod *et al.* 2003). Especially in Japan and other East Asian countries, where rice is a staple food, loss or degradation of traditional ecosystems as well as changes in farming practices has been recognized as major cause of rapid declines in aquatic organisms including plants, invertebrates, fish, and amphibians (Kobori & Primack 2003; Washitani 2001). Therefore the restoration of these aquatic habitats has been an urgent issue in conservation (Primack *et al.* 2000; Washitani 2003).

In a habitat restoration planning, it is important to know, at larger spatial scale, how likely a place is colonized by individuals of focal species (i.e., immigration potential of individuals) when it is restored as a suitable habitat. The immigration potential of individuals is defined as "expected colonization rate of individuals" to a certain restored place, and is a function of patch connectivity and source size at meta-level. However, because many aquatic invertebrates or amphibians have complex life cycles, the connectivity and thus immigration

potential of them would be affected by both spatial arrangement of multiple habitat types and habitat use pattern of the organisms.

Dragonflies are one of the major aquatic taxa inhabiting the traditional rice agricultural ecosystem in Japan. However, forty-one dragonfly species among total 196 Japanese species are now considered to be rare or endangered (Environmental Agency of Japan 2001). Dragonflies have complex life cycles, shifting from aquatic to terrestrial habitats in their adult stage. During their pre-reproductive phase at adult stage, individuals are compelled to move between two types of habitats, from aquatic to terrestrial areas and back again. In the pre-reproductive phase, many dragonfly species use woodlands or forests as suitable habitats for foraging, resting, and avoiding unsuitable (dry and/or hot) conditions (e.g., Fincke 1992; Morton 1977; Watanabe *et al.* 2005). Therefore it is likely that they needs a combination of both aquatic and terrestrial habitats to maintain viable populations.

My previous study (Kadoya *et al.* 2004) demonstrated that the abundance of lentic dragonfly individuals at the newly created habitats was affected by local environmental characteristics of the habitat pond including its size and vegetation cover (Chapter 2) and surrounding landscape structure such as other aquatic and terrestrial habitats (Chapter 3). In addition, differential responses to the landscape structure were suggested between life history groups, that is, more sensitivity of 'long-phase species' with the relatively long pre-reproductive phase of more than 1 month to the amount of woodland habitats around sampling ponds, then 'short-phase species' with pre-reproductive phase of less than 10 days were not (Chapter 3).

Taking into account these results and general dragonfly ecology, I can expect that the immigration potential of dragonflies at landscape scale would be influenced by spatial arrangement of aquatic and terrestrial habitats. The immigration potential would be higher if the both habitat types were abundant in a dispersal range of dragonfly individuals, whereas become lower in the situation where the availability of either habitat type was limited. The magnitude of effects of the spatial arrangement of habitats on the immigration potential would differ between the life history groups.

One approach to analysing and understanding such complex spatial problems in fragmented landscape is the use of spatially explicit simulation models (e.g., Dunning *et al.* 1995; e.g., Turner *et al.* 1995; Wiegand *et al.* 2004a; Wiegand *et al.* 1999). This type of models are promising for providing a powerful tool for analysing the impact of spatial processes and landscape structure on organisms' dispersal (e.g., Mooij & DeAngelis 2003; Vuilleumier & Metzger 2006; Vuilleumier & Perrin 2006). In the present chapter, I present a spatially explicit dispersal model to predict immigration potential of individuals of dragonfly species over the landscape, and compared the predicted immigration potential of dragonflies with two life history groups between two landscapes with different spatial arrangements of aquatic and terrestrial habitats.

The model includes a detailed representation of landscape structure including newly restored habitats, other aquatic and woodland habitats, and permits the simulation of individual movements between landscape features according to dispersal ability and behavior, which are highly dependent on their life history group (Corbet 1999). In order to estimate reliable model parameters

and to reduce model uncertainties, I employed 'pattern-oriented modeling approach' (Wiegand *et al.* 2003; Chapter 1) and, as constraints of the model, used the patterns of immigration of individuals observed at small ponds which were newly created in a restoration project.

Methods

Study site and data sampling

Around Lake Kasumigaura (lat 36°N, long 140°E) in Ibaraki Prefecture, eastern Japan, a considerable number of small shallow ponds were created between 1999 and 2003 to promote the restoration of habitats for dragonflies and endangered aquatic plants in wetland restoration activities shared by local NGOs and schools (Washitani 2003). The ponds have maximum depths of about 40 cm, have gently sloped borders, and are sparsely fringed by aquatic plants such as *Nymphoides peltata* (Gmel.) O. Kuntze, *Sparganium erectum* L., *Bolboschoenus fluviatilis* (Torr.) A. Gray, and *Marsilea quadrifolia* L. that were introduced from nearby wetlands or abandoned paddies. The ponds are supplied with water as the need arises to prevent them from drying out.

I conducted periodic censuses of adult dragonflies during the season of adult dragonfly activity at 10 ponds in the area of Ishioka and other 12 ponds in the area of Hokota for four years (2001 - 2004) and for two years (2003, 2005), respectively. All the 22 ponds were created at the winter of 2000 - 2001. To cover the whole period of activities of all phenological groups (from spring species to late summer and autumn species), I conducted a census of each pond at a frequency of once or twice per month from May to November for Ishioka area

and once per two month for Hokota area. During each census, I walked along the border of the pond and recorded the occurrence and abundance of all individuals encountered. Dragonflies were identified to species level without capturing them, but I occasionally captured them using insect nets when it was difficult to identify individuals by sight. Species were classified as either 'long-' or 'short-phase species' according to the length of pre-reproductive phase. Long-phase species have pre-reproductive phase of more than 1 month before they returning to aquatic habitats to reproduce, whereas short-phase species have a short pre-reproductive phase of less than 10 days (see Chapter 3 for detail). The abundance data from each census was pooled for each species group for each sampling pond for each year.

Vegetation cover (including any type of aquatic plant) of each censused pond was recorded using 10% increments at each census time.

Model structure

I developed an individual-based dispersal model of dragonflies coupled with vector-based realistic representation of landscape structure. In the model, dragonfly individuals disperse over the landscape to seek their habitats with the time step of one day.

Landscape model. The landscape model was constituted on the following basic vector data. I selected *a priori* two types of habitat patch: the irrigation ponds or other small reservoirs (hereafter 'aquatic patch') and woodlands including deciduous and evergreen woodlands (hereafter 'woodland patch'). Aquatic

patches are likely to include habitats for larvae of the dragonflies in the study region, whereas woodland patches would provide summer or winter habitats for adults. The remaining area in the landscape was assumed to be unsuitable habitats for dragonflies (i.e., matrix).

The land cover was represented by mutually exclusive polygons using ESRI ArcGIS 9.0 software (Environmental System Research Institute, Redlands, CA, USA). The distribution of aquatic patches was determined from a 1:25 000 scale digital topographic map (Geographical Survey Institute of Japan), and the distributions of woodland patches was obtained from 1:50 000 scale national land-cover data (sites sampled around 1998; Environment Agency of Japan).

I considered the habitat patches located within 10 km from the nearest sampling ponds for each area.

Emergence and dispersal of dragonflies. My dispersal model comprises movement, mortality and habitat use of dragonfly individuals with the time step of one day. The variables and parameters used in the simulation are listed in Table 4-1.

Individuals emerge from ponds at the numerical proportion to the area of the pond with a slope of α. I considered the area within 1 m from the shore line as an effective pond area because most of larvae of lentic dragonflies are known to inhabit shallow water preferentially (up to several dozen centimeters in depth). In the model, the age 1 or 2 were assigned to each 'virtual' sampling pond (hereafter 'virtual pond') corresponding to the age of 'real' sampling pond (hereafter 'censused pond') from the creation. Individuals were assumed to emerge from the

virtual pond only if the age of the pond was more than 1.

Position of an individual is described by a pair of x, y coordinates to allow for a vector-based movement definition. Individuals move by a distance d in a direction of an angle θ in one step. Two parameters, turn angle (θ) and dispersal length (d), are drawn from random distributions and define successive values of the x, y coordinates for that individual:

$$\theta \sim \mathbf{N}(0, \sigma^2)$$

$$d \sim \mathbf{Ex}(\lambda)$$

where **N** and **Ex** means a normal distribution and a exponential distribution, respectively.

Before the individual is moved, a random number between 0 and 1 is allocated and compared to a given survival parameter value (s). If the random number is larger than the survival parameter value, the individual 'die' and is deleted from the following simulation processes.

An individual has a perceptual area within which they can recognize their habitat patches during dispersal. The perceptual area is formed at each step as a buffer polygon created around a path line with a radius of the individual's perceptual range (δ). The path line is straight and links start and arrival points of a single step movement of the individual. If a part of the perceptual area overlaps with some part of a habitat patch, the individual 'find' the patch to colonize into the habitat. When more than one habitat patch are detected simultaneously, the colonizing patch is selected randomly.

Adult dragonflies are known to disperse away from their natal habitat immediately after their emergence. The behavior is called "maiden flight" (Corbet

1999). In order to consider the behavior, individuals were assumed to disperse until they cannot 'see' their natal aquatic patches – that is, until their perceptual areas do not overlap with the natal aquatic patches, before they begin to search their habitats.

I dealt with two life history types separately in my simulations according to their relative length of pre-reproductive phase i.e., 'long-phase' species and 'short-phase' species. Long-phase species was assumed to have longer life time (L^l) and utilize woodland patches for adult habitat before entering aquatic patches. On the other hand, short-phase species was assumed to shorter life time (L^s) and not necessarily use woodland patches for habitats.

Individuals move independently from each other, i.e., no density effects or interactions between them are considered. Habitat patches are always accessible and are not blocked for further immigrants by previous immigration or carrying capacity.

In contrast to most other existing models, I did not use any kind of border to restrict the landscape. The animals were allowed to run out of the patch-containing landscape and to return as long as they were still alive. This seems biologically reasonable, because a real landscape does not necessarily have edges between patch-containing and empty matrices that are apparent to dispersing animals. In addition, from an analytical viewpoint, omitting borders means the system is not made additionally complex by extra border effects.

The model was implemented using Java coupled with the libraries for individual-based modeling (Recursive Porus Agent Simulation Toolkit 3.1; Repast) and for vector-based spatial analysis (The JTS Topology Suite 1.5; JTS).

Simulation

Parameter ranges. I varied the five parameters in the simulation as listed in Table 4-1.

The value of α, which determines area dependency of the number of emergent individuals, was varied from 0.0 to 0.1 (individuals/m^2). I added a constant number of individuals to each pond so as to regulate the total number of individuals in a simulation run. Because of the computational limitation, I regulated the total number of emergent individuals around 20 000.

The relationships between the probability of dispersal of several dragonflies and distance they moved were reported to consistently follow a negative exponential curve (Conrad *et al.* 1999). We varied the mean value of daily movement distance *dm* from 50 to 500 m, which covers reported daily or life time dispersal distances of dragonflies (e.g., Conrad *et al.* 1999; Purse *et al.* 2003; Watanabe *et al.* 2004; Watanabe & Taguchi 1988).

Because information on turn angle is scarce in the literature, we varied the σ^2 over wide range, from 1 to 90° which ranges from highly directed dispersal to relatively undirected dispersal.

Polarized light reflected by water has been suggested as an important trigger inducing the recognition of an aquatic habita by aquatic insects (Schwind 1991, 1995). That is true for adult dragonfly species (Bernath *et al.* 2002). Perceptual range (δ) should be affected by the flight height and thus the minimum grazing angle from which the dragonfly can detect the reflected light from the water surface. Provided that dragonflies can detect the reflected light from a

relatively small grazing angle of view, 20° for example as examined by Bernath *et al.* (2002), perceptual range (δ) varied from 50 to 200, which are corresponded to the flight height of 18 to 73 m, is reasonable as a height of dragonflies dispersion (Corbet 1999).

I varied survival rate (s) from 0.6 to 1.0 which covers the range of the observed survival rate of various adult dragonflies (e.g., Watanabe *et al.* 2004; Watanabe & Taguchi 1988).

Sensitivity analysis and model predictions. In order to analyze the sensitivity of model predictions to the model parameters, I created parameter sets by drawing random values for the 5 uncertain parameters listed in Table 4-1, independently of each other, from uniform distributions within the ranges given in Table 4-1. The range of variation of each parameter reflects the degree of uncertainty in its estimate. I performed 2048 simulations as a replication for each combination of 3 treatments i.e., two life history groups (long and short-phases), two pond ages (age 1 and older than 1) and two sampling areas (Ishioka and Hokota) except the treatment of pond age 1 at Hokota area which we didn't have the corresponding observed data. Therefore, I performed a total of 12 228 simulations in the present study.

To investigate the sensitivity of the model output to the parameters values, we performed multiple linear regressions with each of 7 model predictions listed in Table 4-2 as the dependent variable and the 5 parameters as independent variables (McCarthy *et al.* 1995). The resulting regression equation relates the parameters of the dispersal model to predicted variables. Because I sampled the

parameter space randomly, multicollinearity should not occur. I scaled the dependent and independent variables to values between 0 and 1 and used the resulting coefficients β_i of the linear regression as indices of the sensitivity of the model output to the parameters p_i . A coefficient $|\beta_i| = 1$ indicates strong sensitivity, while parameters with small values $|\beta_i| << 1$ have little impact on the model prediction. To perform a rough sensitivity ranking of the model parameters p_i , I calculated the average of $|\beta_i|$ for all 7 model predictions.

Calibration using observed data. Patterns produced by the model are systematically compared with the patterns observed in the field. I used the 6 data sets from field observations on immigration of dragonflies to the censused ponds for model calibration. To assess whether or not simulated patterns match the observed pattern, I need to measure the deviation between the patterns, and I need a criterion to define confidence intervals for accordance between the patterns. This criterion acts as a 'filter' for implausible model parameterizations.

To measure the deviation between the simulated number of immigrants to each virtual pond with corresponding observed data at censused ponds, I used an error index calculated by the following equation:

$$E^{ind} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}[Obs_i - Exp_i]^2}$$

where n is the number of the censused pond in the data set, Obs_i is the standardized observed and Exp_i is the standardized expected number of immigrants to censused and virtual pond i. respectively. In order to remove the effects of differences in the internal pond characteristics on the dragonfly

abundance, the observed abundance was regressed on pond size and vegetation cover following the results of Kadoya *et al.* (2004) and the residuals of the regression were used as the corrected observed abundance.

I defined an acceptance threshold for E^{ind} using a randomization approach, and compared E^{ind} to a null model of random immigrants. For this purpose, I created the random distribution of immigrants among virtual ponds by distributing the same total number of individuals expected in the simulation run to the virtual ponds randomly. Using the random distribution, I calculated E^{random} analogously to the calculation of E^{ind}. I repeated this procedure 5000 times to obtain the distribution of E^{random} and use the criterion that E^{ind} should be smaller than the 95.0% range of E^{random} distribution.

Impact of stochasticity on model predictions. To obtain an estimate of the variability of the model predictions due to stochasticity, I repeated the simulation 50 times with the same model parameterization for each life history group at Ishioka area of Age 1 ponds. I assessed the impact of stochasticity on model predictions for six model parameterizations which were randomly chosen among the 10 best ones. For each model parameterization I calculated the resulting mean (mean) and standard deviation (SD) of the 50 replicate estimations for each model prediction. We used the average of the coefficients of variation CV=SD/ (mean of the six model parameterizations) to reflect uncertainty due to stochasticity.

Mapping of immigration potential

In order to map the distribution of immigration potential at the landscape scale, I

located virtual observers at an interval of 2 km and recorded the number of immigrants into each pond through a simulation run using the selected parameter sets. The observers count the number of individuals which 'find' the observer. Each observer does not count the same individual which was previously detected. I repeated the procedure for each selected parameter set and mapped the mean number of observed individuals at each observer's place as an estimate of immigration potential. In addition, I examined the relationships between the number of individuals observed by each virtual observer and the amount of woodland patch and aquatic patch within 1 km in radius from the observer by multiple regression. Because many dragonflies were known to prefer the shoreline of ponds or the edge of woodlands (Corbet 1999), I used the perimeter of habitat patch as index of the amount of available habitats.

Results

Parameter sensitivity

As expected from the large parameter uncertainty, model predictions varied over wide ranges (Appendix 4-1). This high uncertainty in model output was reflected in the high standard deviation of the model predictions. However, I found that the multiple regression models represented satisfactorily high R^2 values ($R^2 > 0.530$).

I found marked sensitivity rankings for both long and short-phase species (Appendix 4-1). The average sensitivity coefficients showed that the mean dispersal distance (d_m) and survival rate (s) were more sensitive model parameters than the other ones irrespective to the life history groups. These two parameters were positively related to *Dist_mean* in any case. Survival rate was also positively

related to *S_rate*. Perceptual range (δ) had lower sensitivity on average but was positively related to *Ind_obs* in any case of pond age or life history type. Area dependency (α) had lower sensitivity as a whole. The parameter with the lowest sensitivity was the step angle for both life history groups.

Effects of stochasticisy

My model showed demographic stochasticity. For six predictions (*Dist_mean, Disp_sd, S_rate, Ind_obs, Ind_obs_SD* and *H_rate*), the coefficient of variation CV ranged below or around 0.05 for both long and short-phase species groups, indicating a relatively low impact of stochasticity. I found CV = 0.19 with *Ind_pond* for long-phase species and CV = 0.45 for short-phase species. However, uncertainty in model predictions ascribable to the stochasticity was roughly one order of magnitude smaller than the variability due to the parameter uncertainty (Appendix 4-1).

Model performances and appropriate ranges of parameters

I compared the number of immigrants to sampling ponds expected from the simulation with the observed ones in the six data sets and selected the parameter sets that yielded smaller E^{ind} value than 95.0 % of E^{random}. The number of parameter sets selected using each data set was shown in Table 4-3. Excluding the duplication, 50 and 382 sets among 2048 parameterizations were selected for long and short-phase species, respectively. The average value of each parameter for each species group was shown in Table 4-4. Long-phase species had the mean dispersal distance (d_m) which was about 100 m longer than that of short-phase

species. *S_rate* and *Dist_mean* predicted by the selected parameter sets were shown in Fig 4-1. Long-phase species had lower *S_rate* and longer *Dist_mean* than short-phase species.

Distribution of the immigration potential

Using each parameter set selected through the calibration of the model prediction with the observed pattern, I ran the simulation and recorded the number of individuals observed by virtual observers located at an interval of 2 km at the landscape. I averaged the number of individuals for each observation points for each species group and assigned the value to the landscape maps of Ishioka and Hokota (Fig 4-2). I found that the total number of potential immigrants of long-phase species at Hokota was relatively small.

The relationships between predicted immigration potential by the model and the perimeter of woodland patch and aquatic patch were shown in Table 4-5. In both areas, the woodland perimeter had stronger effects on the immigration potential of long-phase species than that of short-phase ones, whereas the pond perimeter had stronger positive effects on the immigration potential of short-phase species than that of long-phase ones. Interactions between the woodland and pond perimeters had significant effects only in Hokota area. The interaction had positive effects on the immigration potential of long-phase species, whereas had negative effects on that of short-phase ones in Hokota area.

Discussion

Determinants of immigration potential at landscape scale

Distribution pattern of conspecific organisms over the landscapes is apparently composite results of the environmental constraints, dispersal process and biological interactions. Therefore in order to make a credible prediction of the distribution, a mechanistic model taking into account these causing processes would be needed in many cases. I constructed a simple mechanistic simulation model, describing flight movement of dragonflies and combined with a rather realistic landscape structure, to attempt to predict immigration potential of dragonfly at the landscape with the virtual observers who were positioned at regularly arranged points and counted the number of immigrants to the individual points. I examined the relationships between the predicted immigration potential patterns and spatial arrangement of habitat patches in relation to life history characteristics of dragonfly individuals.

Based on the simulation assumptions, the immigration potential of long-phase species is expected to depend on both the distribution of woodland and aquatic patches, whereas the immigration potential of short phase species is expected to depend on only the distribution of aquatic patches. The results of the multiple regression with the number of immigrants as dependent variable and the amount of woodland and aquatic patches as independent variables roughly follow the expectations, which indicated that the constructed model performed properly.

I found, however, two deviations from the expectation based on the model assumptions. One is that at Ishioka area not only amount of aquatic patch but also woodland patch were significantly related to the immigration potential of short-phase specie though they were assumed not to use the woodlands. The pseudo-correlation arose probably due to the spatially autocorrelated occurrence

of landscape components. As discussed in chapter 3, similar land-use pattern tends to co-occur in a landscape. For example, a landscape with larger urban area is naturally scarce of both woodlands and ponds. The result indicates that the relationship detected by a statistical analysis does not necessarily represent a meaningful relation, and a care should be taken about the pseudo-relationships especially when one treats the spatially autocorrelated landscape components in a statistical analysis.

The other deviation is that, only at Hokota area, interaction between amount of woodland and aquatic patches was positively significant. Taking into account the fact that the predicted number of immigrants of long-phase species was less compared to the other cases, Hokota landscape had woodland and aquatic patches distributed disproportionately, and may have been not easier to disperse for long-phase species than Ishioka landscape.

Relationships between connectivity and life history characteristics

Recently, it has been recognized that the connectivity of animals dispersing actively at landscape can not be predicted satisfactorily by simple indices, especially in the case where individuals show complex responses to the landscape structure (Winfree *et al.* 2005). This should be true for organisms having complex life cycles (Wilbur 1980) and changing the habitat types ontogenetically. In fact, it was elucidated that dragonflies which had different life history characteristics responded to landscape structure differently (Chapter 3).

In the present study, I compared two life history groups (i.e., long-phase and short-phase species) for model performances. It was demonstrated that the

mean dispersal distance (d_m) of long-phase species selected through the calibration was longer than that of short-phase species. In addition, the simulation using the selected parameter sets predicted that long-phase species had lower dispersal success rate (*S_rate*) and longer dispersal distance for colonization (*Dist_mean*) than short-phase species. These facts suggest that the length of pre-reproductive stage and related behavioral characteristics strongly affect the connectivity for dragonflies even at the same landscape.

Pattern-oriented modelling and model performances

The one of advantages of the approach I employed "pattern-oriented approach" (Wiegand *et al.* 2003), is that the effectual ranges of parameters in the model can be estimated indirectly by the calibration of the model prediction with the observed pattern at higher organization level (e.g., population dynamics and distributional pattern over the landscape) (Wiegand *et al.* 2003). In the present study, the parameters concerning dispersal distance or perceptual range, which are usually difficult to measure in the field, were estimated from referring the model prediction to the observed pattern of immigration to the sampling ponds.

The results of sensitivity analysis demonstrated that mean dispersal distance and survival rate had significant effects on the model predictions. The value of the two parameters estimated by the calibration with the observed patterns were also consistent with the values obtained from previous measurements (Watanabe *et al.* 2004; Watanabe & Taguchi 1988). Dispersal distance for colonization (*Dist_mean*) predicted using the parameter sets selected by the calibration was also consistent with the results of previous studies (e.g.,

Conrad *et al.* 1999; Wildermuth & Knaus 2002). However the estimated parameters were still varied in wider ranges. One of the possible reasons is that the information derived from the observed pattern was not enough to regulate the parameter range. In order to solve the problem, it would be needed to add more observed patterns as the calibration filters. Another possible reason is due to demographic stochasticity, though the effects of stochasticity on the model predictions were evaluated not to be so serious in the stochasticity test. The effects of demographic stochasticity can be reduced by running the simulation for more than several times with the same parameter set and using the mean value of the predictions among the replications in the calibration.

More parameter sets were selected for short-phase species than for long-phase species. This is probably due to the lacking sufficient constraints imposed from life historical requirements for short-phase species than long-phase species. Another reason is higher dependence on the characteristics of individual censused pond in short-phase species (Chapter 3) than that of long-phase species. In the present study, I used the observed data in the calibration after the effects of the pond characteristics (i.e., pond surface area and vegetation cover) were accounted for. Therefore, there is possibility that less information was contained in the field data for short-phase species.

It also can not to be denied that the uncertainty of model structures was larger in the model for long-phase species. The model structure was more complex for long-phase species because they were assumed to use woodlands for adult habitats. In the present study, it was assumed that the woodland patches have the same quality. If a dragonfly individual actually responds to woodland

patches differently according to their quality, it is likely that the model which is not consider such behaviors cannot reproduce the observed pattern better for long-phase species than for short-phase species.

Simulation models as tools for restoration planning

For an effective habitat restoration planning, it is important to predict the immigration potential at larger spatial scale to prioritize the large number of candidate sites for restoration. In the decision making process of the restoration planning, a simulation model with a realistic landscape as used in the present study would be potentially useful because it enables us to predict the immigration potential of organisms at any place within the modeled landscape. It is also advantageous to construct a prediction model because, using the model, a dynamic cycle with feedback loops between data collections after the habitat restoration and model predictions can be created, which would enhance further improvement of the model structure and parameter estimation and increase reliability of the model predictions for the following restoration projects.

Table 4-1. Parameters and variables used in the model simulation. Boldface indicates parameters, which are varied in the simulations. L^l and L^s represent life times for long-phase and short-phase species, respectively.

Prameter	Symbol	Range
Emergent number at pond *i*	n_i	
Dispersal distance (m)	d	
Turn angle (degree)	θ	
Life time (step)	L^l, L^s	90, 30
Area dependency (/m^2)	$\boldsymbol{\alpha}$	**0.0 - 0.1**
Mean distance (m)	$\boldsymbol{d_m}$	**50 - 500**
Variance of Turn angle (degree)	$\boldsymbol{\sigma^2}$	**1 - 90**
Perceptual range (m)	$\boldsymbol{\delta}$	**50 - 200**
Survival rate (/step)	$\boldsymbol{s}$	**0.6 - 1.0**

Table 4-2. Symbols used in the description of the model.

Symbol	Meaning
Dist_mean	Mean dispersal distance for successfully colonized individuals
Disp_sd	Standard deviation of *Dist_mean*
S_rate	Success rate of colonization
Ind_pond	Total number of individuals colonzing the sampling ponds
Ind_obs	Total number of individuals observed by virtual observers
Ind_obs_SD	Standard deviation of *Ind_obs*
H_rate	Homing rate within individuals colonized successfully

Table 4-3. The number of parameter sets selected through the calibrations with the six data sets. Using a randomization test, the parameter sets which can reproduce the observed immigration pattern significantly (5 % level) were selected (see text for detail).

Filter	Number of selected parameter set (/2048)
Long-phase species	
Ishioka2001	15
Ishioka2002	12
Ishioka2003	7
Ishioka2004	5
Hokota2003	4
Hokota2005	11
Short-phase species	
Ishioka2001	112
Ishioka2002	12
Ishioka2003	9
Ishioka2004	61
Hokota2003	42
Hokota2005	177

Table 4-4. The mean and the standard deviation of the model parameters selected through the calibration. For symbols of model parameters, see Table 4-1.

	Parameter				
	δ	d_m	σ^2	s	α
Long-pahase species	125.1 ± 48.5	371.7 ± 118.9	47.29 ± 27.34	0.7575 ± 0.1270	0.0571 ± 0.0249
Short-phase species	122.1 ± 40.7	283.2 ± 135.0	44.87 ± 25.75	0.7907 ± 0.1130	0.0504 ± 0.02919

Table 4-5. Results of multiple regressions with the number of potential immigrants as a dependent variable and the woodland and pond perimeters within a radius of 1 km from each virtual observer as independent variables. Const., WP and PP represent constants, woodland perimeter and pond perimeter, respectively.

	Coef.	SE	Coef/SE	t-value	p-value
Ishioka					
Long-phase					
Const.	4.156	0.480	8.662	8.662	< 0.0001
WP	0.339	0.042	8.161	8.161	< 0.0001
PP	2.795	0.430	6.499	6.499	< 0.0001
WP×PP	0.075	0.059	1.274	1.274	0.205
Short-phase					
Const.	2.413	0.460	5.244	5.244	< 0.0001
WP	0.167	0.040	4.198	4.198	< 0.0001
PP	4.214	0.412	10.216	10.216	< 0.0001
WP×PP	0.101	0.056	1.804	1.804	0.073
Hokota					
Long-phase					
Const.	-0.112	0.192	-0.582	-0.582	0.562
WP	0.084	0.011	7.399	7.399	< 0.0001
PP	1.343	0.088	15.309	15.309	< 0.0001
WP×PP	0.089	0.008	10.685	10.685	< 0.0001
Short-phase					
Const.	3.619	0.526	6.878	6.878	< 0.0001
WP	0.028	0.031	0.889	0.889	0.375
PP	4.678	0.240	19.454	19.454	< 0.0001
WP×PP	-0.116	0.023	-5.107	-5.107	< 0.0001

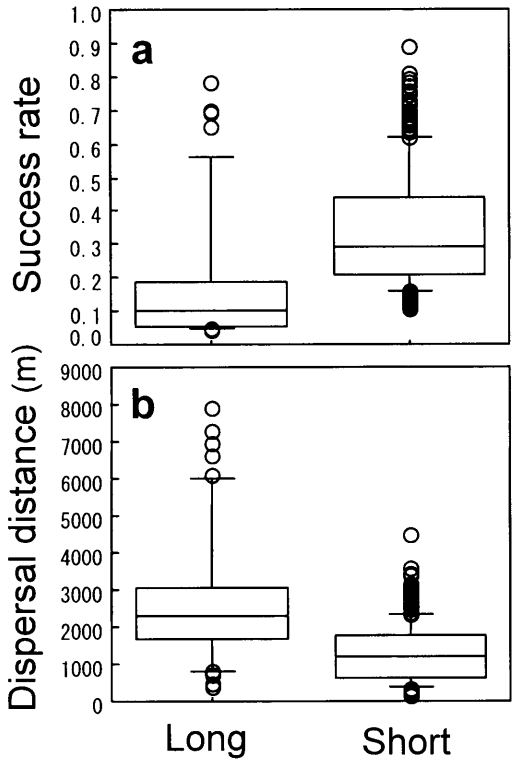


Figure 4-1. (a) Mean colonization success (*S_rate*) and (b) dispersal distance for successful colonization (*Dist_mean*) predicted by the model with selected parameterization in the calibration for long and short-phase species.

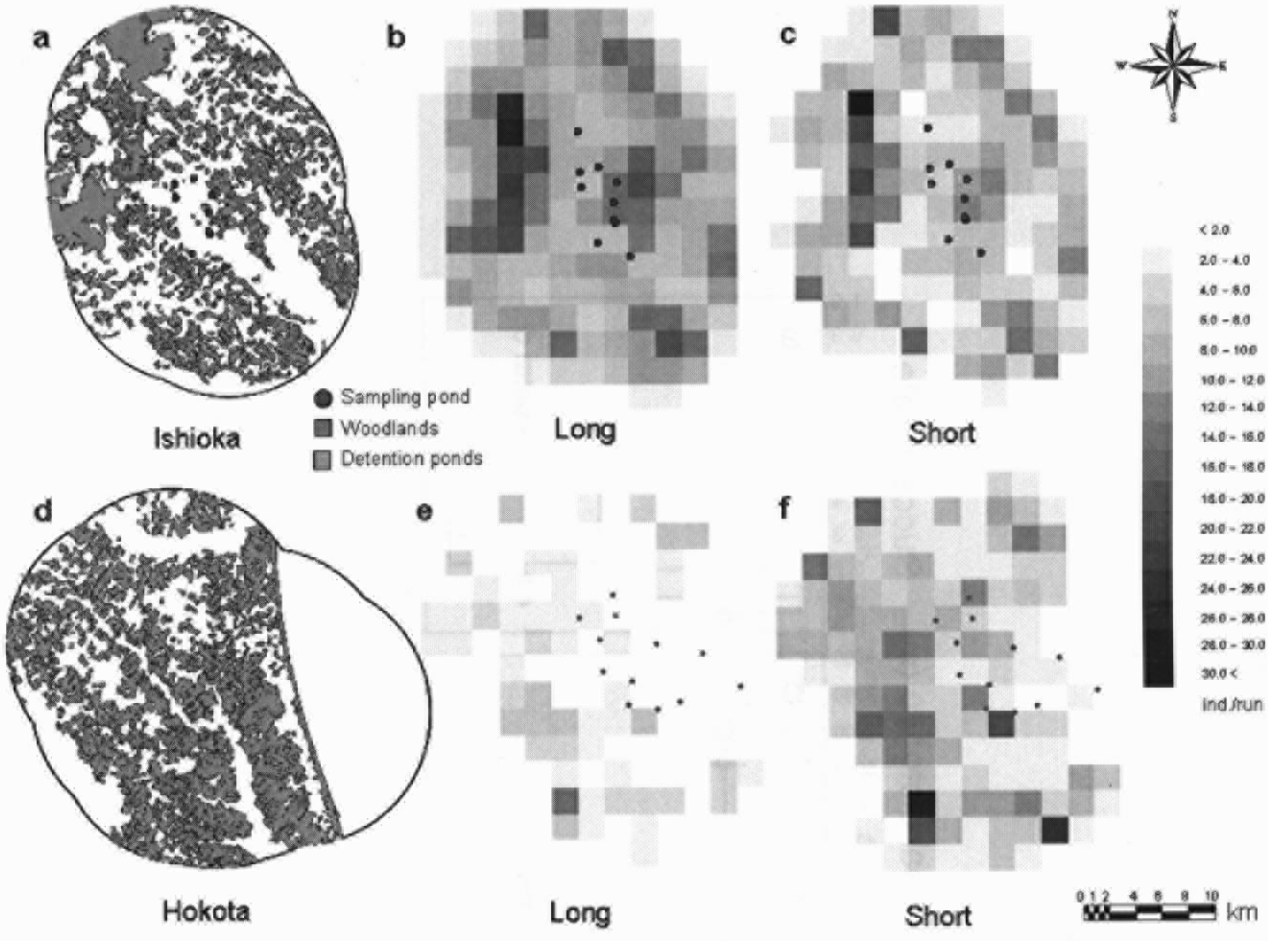


Figure 4-2. Landscape structure and predicted immigration potential at Ishioka and Hokota area. The maps at left column represent distribution of habitat patches at real landscape structure for (a) Ishioka and (d) Hokota areas. Red circles, green and blue polygons represent sampling ponds, woodlands and detention ponds, respectively. The maps at the center column represent pattern of immigration potential for long-phase species at (b) Ishioka and (e) Hokota areas. The maps at right column represent pattern of immigration potential for short-phase species at (c) Ishioka and (f) Hokota areas. The color strength of each grid corresponds to the magnitude of immigration potential. White and black color represent immigration potential of below 2 and over 30 individuals per simulation run,

respectively.

Appendix 4-1. Sensitivity analysis of model predictions based on $n = 2048$ random model parameterizations. Given are the mean ± the standard deviation, the minimum and the maximum value of the model prediction, the R^2 of the multiple linear regression with the prediction as dependent variable and the 5 parameters as independent variables, and the resulting sensitivity coefficient for each model parameter. For symbols of model parameters and model predictions see Tables 4-1 and 4-2.

Prediction	Mean	SD	Min	Max	R-square	δ	d_m	σ^2	s	α
Long-phase species										
Ishioka Age 1										
Dist_mean	1973	1429	211	9202	0.780	-0.015	0.742	-0.012	0.499	-0.024
Disp_sd	1544	1393	124	8578	0.686	-0.020	0.568	-0.013	0.618	-0.032
S_rate	0.222	0.173	0.039	0.876	0.799	-0.015	-0.002	-0.006	0.894	-0.017
Ind_pond	23	38	0	287	0.530	-0.020	0.389	-0.018	0.625	-0.035
Ind_obs	946	1277	11	11186	0.595	0.231	0.367	-0.013	0.639	-0.029
Ind_obs_SD	943	1274	11	11155	0.595	0.231	0.367	-0.013	0.639	-0.029
H_rate	0.324	0.163	0.060	0.789	0.880	0.007	-0.932	0.009	-0.132	0.029
Ishioka Age 2										
Dist_mean	1981	1438	214	9143	0.780	-0.015	0.740	-0.012	0.501	-0.025
Disp_sd	1551	1399	129	8611	0.688	-0.020	0.568	-0.013	0.619	-0.031
S_rate	0.220	0.172	0.040	0.874	0.796	-0.015	0.002	-0.007	0.893	-0.015
Ind_pond	36	48	0	340	0.577	-0.020	0.266	-0.018	0.716	-0.079
Ind_obs	966	1304	12	11695	0.595	0.231	0.365	-0.014	0.640	-0.033
Ind_obs_SD	964	1300	12	11663	0.595	0.231	0.365	-0.014	0.640	-0.033
H_rate	0.324	0.164	0.064	0.785	0.881	0.009	-0.932	0.009	-0.134	0.027
Hokota Age 2										
Dist_mean	2029	1512	215	9853	0.763	-0.018	0.723	-0.012	0.510	-0.030
Disp_sd	1595	1466	135	9092	0.683	-0.021	0.561	-0.014	0.621	-0.036
S_rate	0.200	0.161	0.035	0.835	0.783	-0.016	0.013	-0.007	0.886	-0.009
Ind_pond	64	68	2	470	0.633	-0.016	0.084	-0.012	0.786	-0.131
Ind_obs	1017	1456	17	13290	0.569	0.212	0.366	-0.015	0.626	-0.037
Ind_obs_SD	1016	1453	17	13264	0.569	0.212	0.366	-0.015	0.626	-0.037
H_rate	0.355	0.174	0.078	0.822	0.885	0.009	-0.933	0.011	-0.149	0.009
Short-phase species										
Ishioka Age 1										
Dist_mean	1195	741	163	4060	0.910	-0.003	0.859	0.004	0.371	0.002
Disp_sd	984	673	110	3572	0.875	-0.004	0.762	0.006	0.502	-0.004
S_rate	0.383	0.179	0.121	0.914	0.923	-0.002	-0.176	0.004	0.954	0.002
Ind_pond	29	35	0	212	0.693	-0.003	0.556	0.008	0.589	-0.018
Ind_obs	844	817	27	5777	0.740	0.370	0.465	0.006	0.605	-0.011
Ind_obs_SD	842	815	27	5761	0.740	0.370	0.465	0.006	0.605	-0.011
H_rate	0.436	0.150	0.168	0.770	0.951	0.004	-0.960	0.008	-0.121	0.037
Ishioka Age 2										
Dist_mean	1199	745	164	4092	0.909	-0.003	0.857	0.004	0.373	0.002
Disp_sd	987	675	109	3600	0.875	-0.005	0.761	0.005	0.503	-0.004
S_rate	0.381	0.179	0.123	0.904	0.922	-0.002	-0.174	0.004	0.954	0.005
Ind_pond	91	55	18	322	0.789	-0.002	0.005	0.007	0.867	-0.201
Ind_obs	869	836	22	5869	0.741	0.371	0.460	0.007	0.609	-0.015
Ind_obs_SD	866	834	22	5853	0.741	0.371	0.460	0.007	0.609	-0.015
H_rate	0.438	0.151	0.172	0.773	0.951	0.005	-0.960	0.006	-0.124	0.034
Hokota Age 2										
Dist_mean	1267	820	158	4479	0.886	-0.005	0.825	0.006	0.409	0.000
Disp_sd	1058	743	115	3819	0.866	-0.006	0.747	0.006	0.515	-0.008
S_rate	0.312	0.166	0.093	0.909	0.844	-0.003	-0.188	0.004	0.909	0.010
Ind_pond	98	63	15	379	0.707	-0.004	-0.170	0.006	0.812	-0.195
Ind_obs	1037	1066	38	8516	0.710	0.335	0.443	0.009	0.616	-0.014
Ind_obs_SD	1035	1063	38	8499	0.710	0.335	0.443	0.009	0.616	-0.014
H_rate	0.420	0.153	0.158	0.824	0.917	0.005	-0.940	0.008	-0.139	0.016
Average sensitivity coefficient of model parameters for long-phase species						0.075	0.460	0.012	0.590	0.035
Average sensitivity coefficient of model parameters for short-phase species						0.105	0.556	0.006	0.562	0.030

Chapter 5 Predicting the trajectory of species recovery based on the nested species pool information: dragonflies in a wetland restoration site as a case study

Introduction

The loss of semi-natural habitats due to agricultural intensification and marginalization of traditional agricultural systems, both of which have led to the abandonment of traditional land uses, is one of the main threats to biodiversity in agricultural ecosystems (Krebs et al. 1999; Ormerod et al. 2003). Especially in Japan and other East Asian countries, where rice is a staple food, loss or degradation of traditional ecosystems and changes in farming practices have been recognized as major causes of rapid declines in aquatic organisms, including plants, invertebrates, fish, and amphibians (Kobori & Primack 2003; Washitani 2001). The restoration of aquatic habitats within the network of paddy fields, ponds, and creeks, which are connected to adjacent rivers or streams, has become an urgent matter in conservation. When planning the restoration of native species assemblages, we should learn not only what type of habitats each organism depends on but also the likelihood of colonizing a site once suitable habitats are restored—that is, their immigration potential from the regional species pool must be considered (e.g., Campbell et al. 2003; Srivastava 2005).

Dragonflies (Odonata) are one of the major taxa inhabiting the traditional rice agricultural ecosystem in Japan (Washitani 2001) and have been widely proposed as indicators of the ecological quality of land–water ecotones, aquatic

habitat heterogeneity (e.g., bank morphology and aquatic vegetation), and the hydrological dynamics of water bodies (e.g., Chovanec & Waringer 2001; Clark & Samways 1996; D'Amico *et al.* 2004). However, it has been demonstrated that the distribution of dragonfly species within a community is strongly 'nested' (Kadoya *et al.* 2004; Sahlen & Ekestybbe 2001); that is, the prevalent species are found everywhere, whereas the rare species tend to occur only at the richest sites (Patterson & Atmar 1986). On a regional scale, this nestedness is likely to be a consequence of species distribution along a site-capacity gradient (e.g., Worthen et al. 1998; Wright et al. 1998). In this context, the site capacity is a function of the habitat heterogeneity within a site and of the quality of each habitat type. For dragonfly assemblages, habitat heterogeneity is determined by the number and the total area of habitat types within a site, such as ponds, bogs, marshes, and creeks, all of which are maintained in a rural agricultural landscape (Washitani 2001), and by the quality of each habitat type, which is likely to be affected by factors such as the water quality, abundance of aquatic vegetation, and presence of predatory fish.

Japan has about 200 resident dragonfly species, and their ecological characteristics have been thoroughly described by Sugimura *et al.* (1999). In addition, data on their occurrence across the country has been documented at a scale of 10 × 10 km in the national database of wildlife distribution (Ministry of the Environment of Japan 2002a). Because the spatial scale in the database is rather coarse, the absolute species richness at any given site is not always reliable (Y. Tsubaki, Kyoto University, personal communication). However, the reported relative species prevalence in a region can be quantified because the detection

rates of different species at each sampling should be related to their abundance hierarchy within the region; thus, species with larger populations are likely to be identified as prevalent, whereas those with a smaller population will be identified as rare. Therefore, in the present chapter, I chose to use the word "rare" for species with smaller and fewer populations in a region, probably as a result of more restrictive habitat requirements. Conversely, I have chosen 'prevalent' as the antonym for rare and have used it for species inferred to have larger and more populations.

If one can confirm the nestedness and quantify the relative prevalence of the species using the database for a region in which a restoration project has been conducted, we may be able to predict the trajectory of species recovery at the restoration site according to species prevalence in the region. Thus, one may be able to suggest which types of habitat should be given priority in the restoration project. In the present study, I developed and tested a procedure to predict the trajectory of species recovery and to prioritize habitat types in a restoration project. I first examined the nestedness of the distribution of dragonfly species in the region using the national database of wildlife distributions of Japan. I then listed the recorded species in order of their prevalence in the region. I also conducted a census of adult dragonflies at the restoration site within the region to assess the current state of species richness. By comparing these data, I identified species potentially capable of inhabiting the site (hereafter, "potential species") and, based on their habitat requirements, suggested what types of habitat should be restored preferentially.

Methods

A nested assemblage model of dragonflies

A conceptual diagram of the nested assemblage of dragonflies is shown in Figure 5-1. Site capacity, which is the capacity of a site to accommodate different species, is a function of habitat heterogeneity within the site and of the quality of individual habitat types. Therefore, sites with higher capacity can support a larger number of species. In a nested assemblage, the prevalent species are typically found at all sites, whereas the rare species tend to occur only at the richest sites (Patterson & Atmar 1986). In other words, sites that support rare species will have a high site capacity and a correspondingly high species richness. The curve that defines the boundary between the presence and absence of a species can be varied from concave-down (as shown in Fig. 5-1) to convex-down depending on species compositions and frequency distributions of site capacities. In either case, the ability to confirm the nestedness of the species distribution allows us to predict which species are likely to occur after a habitat restoration by comparing the current state of the species assemblage at the site with the regional pattern of nested assemblages.

Study site

The Matsu-ura River is one of the largest rivers on Japan's Kyushu Island, with a catchment area of about 446 km^2 and an annual average discharge of about 12.46 m^3/s. The Azame restoration area (33°20'N, 129°59'E) occupies a small part of an old floodplain in the middle reaches of the Matsu-ura River, about 15.8 km from the mouth of the river (Fig. 5-2), and was farmed as rice paddies until 2001.

Starting in 2003, a restoration project was begun in a 6-ha part of the area by the Japanese Ministry of Land Infrastructure and Transport.

Before restoration, the ground level of the Azame area was about 5 m above the normal water level of the river because of the deeply incised main channel, the aggraded floodplain, and regulation of the river's flow path by embankments. Consequently, the connectivity and ecotones between aquatic habitats had been entirely lost. Therefore, the restoration project prioritized solutions that would eliminate this disconnectivity and create ecotones from the river to the study site by lowering the aggraded site and partially removing the embankments. As a second step, restoration of the agricultural aquatic habitats maintained by traditional forms of agriculture, including paddy fields, bogs, ponds, and creeks connected to the river, began in 2005.

Data collection

Regional species list and prevalence. Data on the distributional pattern of dragonfly species in northern Kyushu were obtained from the national database on wildlife distribution (Ministry of the Environment of Japan 2002a). The database includes records of the occurrence of every species at a scale of 5'N × 7'30"E (about 10 × 10 km), called 'the secondary mesh (grid)'; 64 cells of this mesh (i.e., an 8 × 8 grid) combine to make up a larger square of about 80 × 80 km in size, called 'the primary mesh,' that covers all of Japan. I employed the species occurrence data from 320 cells of the secondary mesh included in five cells of the primary mesh (cell ID numbers 4930, 4931, 5029, 5030, and 5031) in northern Kyushu (Fig. 5-2), which cover one of the eco-regions of dragonflies in Japan

(Sugimura et al. 1999).

Species list at the restoration site and nearby habitats. I conducted a census of adult dragonflies from 2003 to 2005 at both the restoration site and nearby habitats, including abandoned rice paddies, ponds, and woodlands (Fig. 5-2). To cover all phenological groups (from the early-spring species to the late-summer and autumn species), the censuses were conducted six times (i.e., late July 2003; late May and mid-September 2004; and mid-May, mid-September, and mid-October 2005) to include the whole season of adult dragonfly activity. In each census, the number of each species were recorded at each site (i.e., the restoration site, the abandoned paddies, the ponds, and the woodland trail; Fig. 5-2). During the census, we walked around each site and identified dragonflies by sight, but also captured individuals using insect nets when the species were sighted for the first time in our census or when it was difficult to identify them from a distance. The total census effort from 2003 to 2005 was 560, 897, 507, and 345 researcher-minutes at the restoration site, the ponds, the abandoned rice paddies, and the woodland trail, respectively. Because dragonfly species exhibit inter-species differences in diurnal patterns, the census was conducted both in the morning and afternoon hours to ensure that we could find all species at each site.

Ecological characteristics of the species. The species-specific habitat requirements of dragonflies in the larval stage and their biogeographic ranges were obtained from Sugimura et al. (1999). In addition, species listed in the national (Environment Agency of Japan 2000) and prefectural (Saga Prefecture

2003) red lists were identified as 'endangered species'. The endangered status of species can be treated independently of the rank order of prevalence in the region because the status was defined by several other criteria as well as prevalence, and by information from different spatial scales i.e., whole country (the national red list) or a single prefecture (the red list of Saga Prefecture).

Data analysis

Test of nestedness. I tested the nestedness of the presence–absence matrix of dragonfly species at the level of the secondary meshes in northern Kyushu using the 'binary matrix nestedness temperature calculator' (BINMATNEST) (Rodriguez-Girones & Santamaria 2006). As defined by the program, a matrix with perfect nesting has a temperature of 0°, whereas the temperature rises as disorder increases. At 100° there is no order left. I performed 5000 Monte Carlo simulations to obtain the probability of a nonrandom distribution. Random matrices were produced so as to preserve the fraction of presence-denoting cells in each column and row of the original matrix (i.e., null model 3 in BINMATNEST).

If the matrix is significantly nested, one may be able to use 'species prevalence', which is the rank order of species in the maximally packed matrix, as a measure of the immigration potential of the species to my study site from the regional species pool. The maximally packed matrix is obtained by permuting the rows and columns of the original presence–absence matrix so as to maximize its nestedness using a genetic algorism implemented by Rodriguez-Girones and Santamaria (2006). On the recommendation of Rodriguez-Girones and

Santamaria (2006), I used a set of parameters in the program i.e., 30, 7 and 2000 for *PopSize*, *TourSize* and *nbGen*, respecticvely, where *PopSize* is 'population size' or the number of possible solutions that are improved by the production of new variants with selection the best-performing ones, *TourSize* is the number of 'individuals' treated at one generation, and *nbGen* is the number of 'generations'or iteration time (see Rodriguez-Girones & Santamaria 2006 for details).

Species occurrence as a function of their prevalence. I ranked all species in order of their prevalence, and used this rank order in our statistical analyses, as described later in this section. All species were categorized into the group of species which were observed at the restoration site (hereafter, 'restoration-site species') and the group of species which were not (i.e., potential species). On this basis, potential species include species observed at nearby habitats (hereafter, 'nearby-habitat species') and those recorded only at the regional scale (hereafter, 'regional-only species'). Species that do not use agricultural aquatic habitats (i.e., in this study, bogs and marshes, ponds, and bodies of water with a slow current) or that do not establish breeding populations in the region were also excluded from the list.

I modeled the probability of occurrence of nearby-habitat and restoration-site species using logistic regression, with the rank order of prevalence as the explanatory variable. In addition, the state of a species in the red book lists (i.e., categorized as endangered or not) for each listed species was modeled by means of logistic regression, with the rank order of prevalence as the explanatory

variable. In the logistic regression analysis, the area under the curve was calculated for each model. This parameter represents the predictive performance of a model evaluated using the receiver operating characteristics technique (Fielding & Bell 1997; Manel et al. 2001). The statistical analyses were conducted using the JMP software (SAS Institute, Inc., Cary, NC, USA).

Target habitats. The potential species were categorized according to their preference for three habitat types (i.e., bogs and marshes, ponds, and bodies of water with a slow current) in the larval stage. To reveal any habitat types that were lacking at the restoration site, I compared the relative proportions of the three habitat types used by nearby-habitat and regional-only species to the proportions for restoration-site species. Because some species used multiple habitat types, the categories were not mutually exclusive. Therefore, I employed a randomization test instead of parametric tests to examine the significance of differences between the ratios.

In the randomization test, I compared the actual proportions with the expected proportions using the same statistic, with a chi-squared test for goodness of fit: $\Sigma(X_i - E_i)^2/E_i$, where X_i is the observed value for habitat type i (i.e., the number of nearby-habitat or regional-only species that use the habitat type divided by the total frequency), and E_i is the expected value for habitat type i (i.e., the number of restoration-site species that use the habitat type divided by the total frequency). I then generated a null distribution of the statistic (n = 10 000) assuming that the potential species were a random assemblage of the restoraiton-site species, and I compared the observed statistic with the null

distribution.

Results

Species distributions

The species database for the north of Kyushu region reports that 154 of the 320 secondary meshes contained at least one species, and the presence of 91 species had been recorded on the database (see Appendix 5-1). An endangered species, *Libellula angelina* (Libellulidae) is probably distributed at the region (S. Suda, the University of Tokyo, unpublished data) but was not included in the list because it was not recorded in the public database for the purpose of conservation. The presence–absence matrix for the 91 species recorded in northern Kyushu represented a significantly nested distribution ($T = 12.4°$, $p < 0.0001$) (Fig. 5-3).

In the censuses conducted from 2003 to 2005, 17 and 52 species were observed at the restoration site and the nearby habitats, respectively (Appendix 5-1). All of these species had been previously recorded in the regional database.

At the restoration site, colonizer species such as *Ischnura senegalensis, Orthetrum albistylum speciosum*, *Pantala flavescens*, and *Anax parthenope Julius*, all of which prefer temporary pools (Kadoya *et al.* 2004; Chapter 2) were frequently observed. However, I only found nationally or regionally endangered species such as *Ceriagrion nipponicum* (Coenagrionidae), *Platycnemis foliacea sasakii* (Platycnemididae), and *Oligoaeschna pryeri* (Aeshnidae) at nearby habitats. At the nearby habitats, I also observed species that are known to require abundant aquatic vegetation in their habitat, such as *Trigomphus interruptus, Rhyothemis fuliginosa*, *Sympetrum croceolum*, and *Sympetrum speciosum*

speciosum, and species that inhabit open marshes, such as *C. nipponicum*, *O. pryeri* and *Sympetrum parvulum*.

Potential species and their habitats

The list of the potential species is shown in Table 5-1. We excluded a total of 36 species from the 91 species recorded on the database. As a result, we listed a total of 55 potential species in Table 5-1 in order of prevalence; this list contained 35 nearby-habitat species and 20 regional-only species. The excluded species were 17 species which were already observed at the restoration site (Appendix 5-1) from the list, 13 species that do not use the rice agricultural habitats (i.e., bogs and marshes, ponds, and bodies of water with a slow current), and 8 species which were 'transient species', species that are non-breeding species in the region (Appendix 5-1). Two species, *Tramea virginia* and *Anax guttatus* were transient species and were observed at the restoration site.

The probability of occurrence of both nearby-habitat and restoration-site species decreased significantly with decreasing species prevalence (Figs. 5-4a, b). However, the probability of occurrence of restoration-site species decreased more rapidly with decreasing species prevalence than that of nearby-habitat species. The probability of occurrence of endangered species increased significantly with decreasing species prevalence (Fig. 5-4c).

There were no significant differences between the habitat-use patterns of restoration-site species (15 species) and nearby-habitat species (35 species; randomization test, n = 10 000, chi-squared p = 0.220) or regional-only species (20 species; randomization test, n = 10 000, chi-squared p = 0.610; Fig. 5-5).

Discussion

Procedure for prediction of the trajectory of species recovery

In this chapter, I proposed a handy procedure for predicting the trajectory of species re-establishing themselves in a newly restored habitat by comparing the estimated nested species pool and the observed current state of species recovery at the target site.

The approach is straightforward and should be applicable to any community having a nested species pool, which is common in many pond-dwelling species (e.g., dragonflies (Kadoya *et al.* 2004; Sahlen & Ekestybbe 2001), such as amphibians (Baber et al. 2004)). Another advantage of the procedure is that it is applicable in situations where appropriate historical data or reference ecosystems are not available, which is often used to establish the end-point of the restoration (Society for Ecological Restoration International Science & Policy Working Group 2004). A list of potential species based on their prevalence, which is derived from the procedure, will provide a comprehensive image of the current state of a restoration site and a flexible and ecologically meaningful guide for the planning of restoration.

Early immigration of dragonfly species

Dragonflies are known to have a nested distribution within a community (Kadoya *et al.* 2004; Sahlen & Ekestybbe 2001). Indeed, in this case study, I also observed significant nestedness in the presence–absence matrix for the dragonfly species in northern Kyushu. Therefore, I can predict roughly that species recovery at the

restoration site will occur approximately in the order of species prevalence in the region. To verify this prediction, an additional census will be needed several years or decades after the restoration operations are complete, since the prediction is only partially supported by the results of the present study due to of the short study duration. This prediction is partly supported, however, by the fact that species observed at the restoration site (i.e., restoration-site species) at this early stage in the restoration process were nested within the nearby-habitat and regional-only species assemblages, and simultaneously had a high prevalence. It would be reasonable to assume that the immigration potential of restoration-site species, nearby-habitat species and regional-only species decrease in this order. The composition of restoration-site species is expected to become more similar to that of nearby-habitat species in the progress of time. In the current early stages, however, it can be assumed that the species with higher immigration potential have a high possibility of occurring in the restoration site. In fact, the configuration of the estimated probability line of restoration-site species was skewed more strongly towards increasing species prevalence.

There remains the possibility that the nestedness test in the present study contains some biases due to opportunistic sampling, which may have affected the national database of wildlife records. However, the rank order of prevalence in the region explained well the occurrence of species and the prediction of early trajectory of species recovery at the restoration site. Therefore, the effects of the biases contained in the database seem to be marginal in the present study.

Prediction of endangered species immigration

At present, none of endangered species occurred at the restoration site, and the probability that the species identified as endangered increased with decreasing species prevalence in the region. These facts indicated that the endangered species had lower immigration potential than other species. In addition, one may be able to quantify the immigration potential of each endangered species based on its prevalence, which is valuable for taxa conservation. Taking into account the immigration potential of the species, the endangered species, *C. nipponicum*, *P. foliacea* and *O. pryeri* are likely to be realistic candidates for re-establishment because they have been already observed at nearby-habitats and have high prevalence relative to other endangered species in the region.

Preferential habitat types

There were no significant differences in the required habitat types between the currently observed species, nearby-habitat species, and regional-only species. All three habitat types (i.e., bogs and marshes, ponds, and bodies of water with a slow current) are planned to be restored during the restoration project. However, the habitat type classification used in the study was rather coarse, and a finer classification based on the quality of each habitat type will be needed in future studies to facilitate the recovery of populations of species with specific habitat requirements.

I should note that frequent updates of the species distribution database are critical for this procedure to be effective because the regional species pool is not always stable. For example, if the regional species pool is degrading due to serious adverse anthropogenic effects on the ecosystem, the immigration potential

of the target taxon could be overestimated. In the present study, prevalent species in the region tended to have a high immigration potential (i.e., they are already observed at nearby habitats). This supports the reliability of the database used in the present study to estimate the immigration potential of the species in the region.

Implications for practice

• Using Japanese dragonflies as a case study, it is demonstrated that the trajectory of species recovery in a newly restored habitat is predictable from the rank order of species prevalence in a regional scale.

• Tests of the nestedness of the species pool and quantification of the rank order of prevalence can be conducted using a database of wildlife records covering an eco-region in which the focal restoration site is included.

Table 5-1. List of dragonfly species in order of prevalence (RP) at the Azame restoration site. Regional species have been recorded in northern Kyushu and their frequencies are reported for the 154 secondary meshes; NH are species observed at the nearby habitats shown in Figure 5-2. 'o' and '+' for occurrence represent species whose abundance was more than four and less than five individuals throughout all census periods at the nearby habitats, respectively. Species listed as endangered in the national (Environment Agency of Japan 2000) and regional (Saga Prefecture 2003) red data lists (RDL) are shown by the rank criteria in the list as VU (vulnerable species) and NT (near-threatened species). The habitat types for each species (BM, bogs and marshes; P, ponds; SC, bodies of water with a slow current) are described according to Sugimura *et al.* (1999) and '+' in the column means that the species was reported to use the habitat type.

Species	RP	Occurrence		RDL		Habitat type		
		Regional	NH	National	Regional	BM	P	SC
Mnais pruinosa	4	62	+	-	-	-	-	+
Copera annulata	6	47	O	-	-	-	+	+
Sympetrum frequens	8	47	O	-	-	+	+	-
Asiagomphus melaenops	9	49	O	-	-	-	-	+
Gynacantha japonica	10	34	O	-	-	+	+	+
Anotogaster sieboldii	11	53	O	-	-	+	-	+
Orthetrum triangulare melania	15	46	O	-	-	+	+	+
Sympetrum eroticum eroticum	19	42	O	-	-	+	+	+
Sympetrum darwinianum	20	39	O	-	-	+	+	-
Davidius nanus	21	30	O	-	-	-	-	+
Pseudothemis zonata	24	39	O	-	-	-	+	+
Macromia amphigena amphigena	25	25	O	-	-	-	+	+
Sympetrum speciosum speciosum	27	30	O	-	-	+	+	-
Anax nigrofasciatus nigrofasciatus	28	35	O	-	-	+	+	-
Indolestes peregrinus	29	31	O	-	-	+	+	-
Stylogomphus suzukii	31	21	-	-	-	-	+	-
Sympetrum parvulum	32	33	+	-	-	+	-	-
Sympetrum pedemontanum elatum	33	27	-	-	NT	+	-	+
Somatochlora uchidai	34	27	O	-	-	-	+	-
Sympetrum risi risi	35	25	O	-	-	-	+	-
Aciagrion migratum	36	22	O	-	-	+	+	-
Ceriagrion melanurum	37	27	O	-	-	+	+	-
Rhyothemis fuliginosa	40	24	+	-	-	+	+	-
Trigomphus citimus tabei	42	24	O	-	-	+	+	+
Polycanthagyna melanictera	43	19	O	-	-	-	+	-
Lestes temporalis	44	22	O	-	-	+	+	-
Sympetrum kunckeli	45	15	-	-	VU	+	+	-
Sympetrum striolatum imitoides	46	13	-	-	-	-	+	-
Sympetrum baccha matutinum	47	19	O	-	-	+	+	-
Anaciaeschna martini	49	19	O	-	-	+	+	-
Sympetrum infuscatum	50	15	O	-	-	+	+	-
Ceriagrion nipponicum	52	20	O	VU	-	+	+	-
Boyeria maclachlani	53	12	-	-	-	-	-	+
Lestes sponsa	54	17	O	-	-	+	+	-
Platycnemis foliacea sasakii	57	14	O	VU	NT	-	-	+
Epitheca marginata	58	16	-	-	-	+	+	-
Sympetrum croceolum	60	15	+	-	-	-	+	-
Mnais costalis	61	10	-	-	-	-	-	+
Trigomphus interruptus	63	15	+	-	-	+	+	-
Asiagomphus pryeri	64	12	-	-	-	-	-	+
Oligoaeschna pryeri	66	14	O	-	NT	+	-	-
Trigomphus ogumai	67	13	-	-	-	+	+	-
Nihonogomphus viridis	68	13	-	-	NT	-	+	+
Gomphus postocularis	69	8	-	-	NT	-	+	+
Sinictinogomphus clavatus	70	15	O	-	-	-	+	-
Aeschnophlebia longistigma	71	12	-	-	-	-	+	-
Cercion sexlineatum	74	8	-	-	NT	+	+	-
Mortonagrion selenion	77	7	-	-	VU	+	-	-
Aeschnophlebia anisoptera	78	6	+	-	NT	+	+	+
Agriocnemis femina oryzae	79	5	-	-	-	+	-	+
Cercion sieboldii	80	5	-	-	-	+	+	+
Aeschna nigroflava	81	4	-	-	-	-	+	-
Lestes japonicus	84	7	-	VU	-	+	+	-
Nannophya pygmaea	86	3	-	-	VU	+	-	-
Sympetrum uniforme	87	3	-	VU	-	-	+	-
Total		55	35	3	10	33	41	21

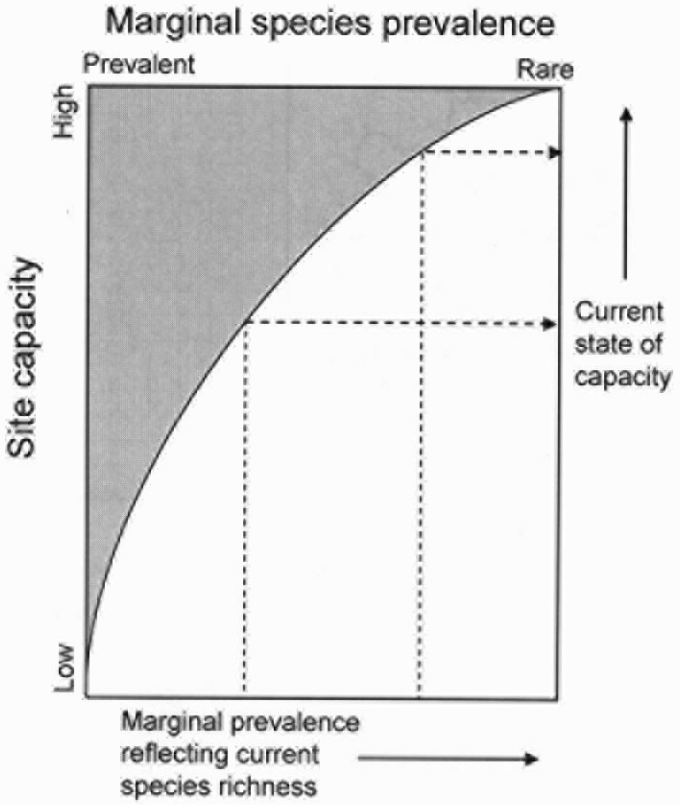


Figure 5-1. A conceptual diagram of the relationship between the nested species assemblage and site capacity (i.e., the number of species a site can support based on its habitat diversity). The shaded area represents the likelihood of species of with different degrees of rarity occurring at the site. Sites with rare species are considered to have a high species richness, and thus to have a high site capacity. The arrows illustrate the direction of improvement in site capacity and species richness. Dashed lines represent the relationship between the marginal prevalence reflecting species richness and site capacity at two points in time.

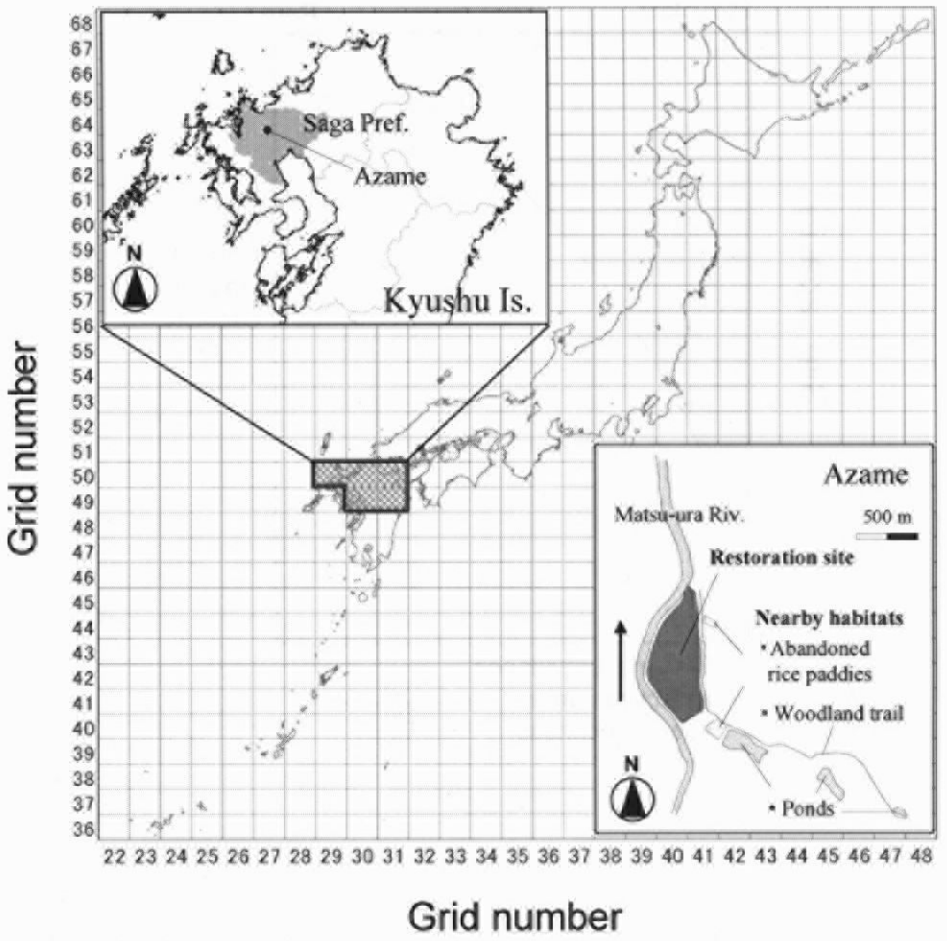


Figure 5-2. Location of the study sites in the Azame restoration area. The larger mesh (grid) represents cells with an area about 80×80 km in size, divided into 64 smaller cells, each about 10×10 km in size. In the present study, we focused on the occurrence of dragonfly species in five of the larger mesh cells (i.e., 320 of the smaller mesh cells) indicated in the shaded area of the map.

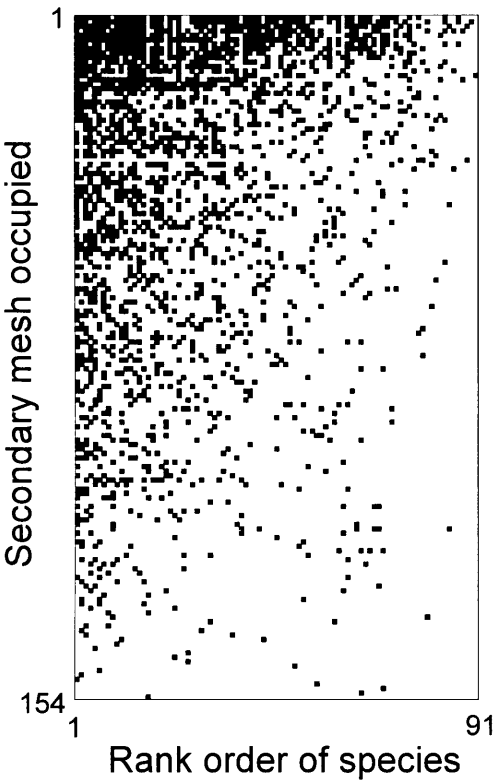


Figure 5-3. The nested distribution of 91 dragonfly species in the 154 secondary meshes in northern Kyushu. A square shaded by black represents the presence of the individual species in the mesh. Ninety one species were apposed to maximize the nestedness of the matrix on the basis of the algorithm proposed by Rodriguez-Girones and Santamaria (2006). The degree of nestedness in the matrix was examined by means of a randomization test (n = 5000 Monte Carlo simulations) using the binary matrix nestedness temperature calculator of Rodriguez-Girones and Santamaria (2006), and significant nestedness (T =12.4°, $p < 0.0001$) was detected.

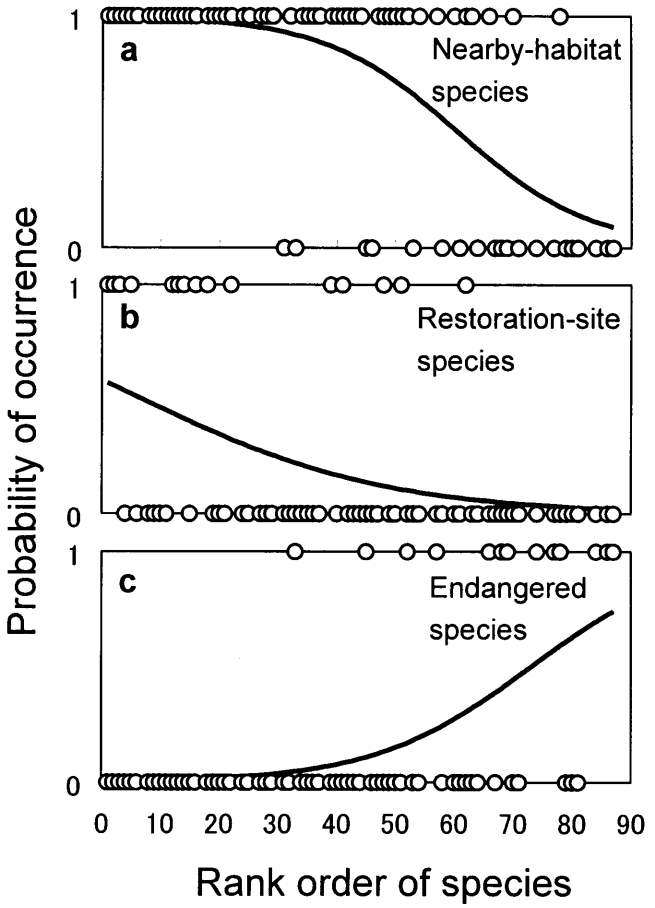


Figure 5-4. Probability of occurrence of dragonfly species (a) observed at nearby habitats, (b) at restoration site and (c) identified as endangered based on logistic regression models using the rank order of prevalence of the species as an explanatory variable. Binary number was assigned to each species based on presence/absence or endangered status (1 = present or endangered, 0 = absent or not endangered) and the number was plotted with line representing the occurrence probabilities estimated by the logistic regression.(nearby habitats: area under curve, AUC = 0.892; likelihood ratio test, $p < 0.0001$; restoration site: AUC = 0.775; likelihood ratio test, $p < 0.001$; endangered species: AUC = 0.863; likelihood ratio test, $p < 0.0001$).

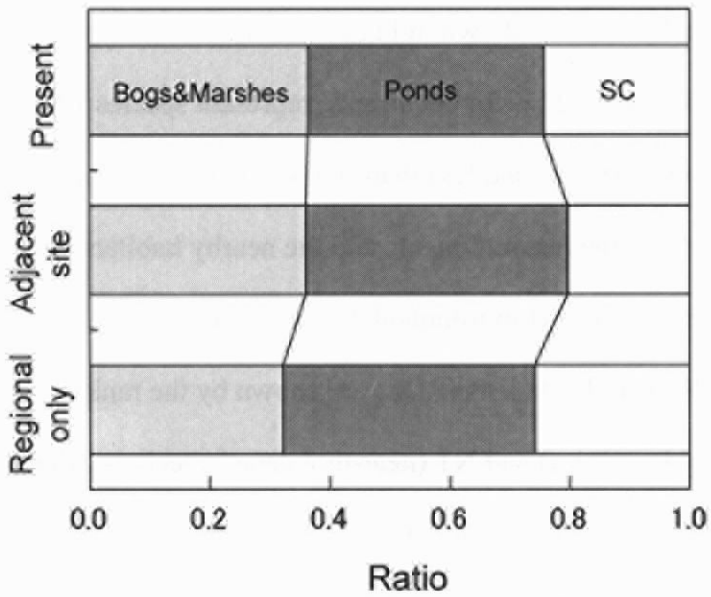


Figure 5-5. Comparison of the proportions of species in the three habitat types (bogs and marshes; ponds; and SC, bodies of water with a slow current) for species observed at nearby habitats, recorded only at the regional scale, and observed at the restoration site. See text for detail.

Appendix 5-1. List of species recorded in northern Kyushu in order of their prevalence. Regional species have been previously recorded in northern Kyushu, and their frequencies are reported for the 154 secondary meshes; NH are species observed at the nearby habitats shown in Figure 5-2 and RS are species observed at the restoration site. 'o' and '+' for occurrence represent species whose abundance was more than four and less than five individuals throughout all census periods, respectively, at the restoration site and the nearby habitats. Species listed as endangered in the national (Environment Agency of Japan 2000) and regional (Saga Prefecture 2003) red data lists (RDL) are shown by the rank criteria in the list as VU (vulnerable species) and NT (near-threatened species). Transient species are non-breeding species found in the region, and NFS are non-floodplain species.

Species	RP	Occurrence			RDL		Nontarget species	
		Regional	NH	RS	National	Regional	Transient	NFS
Orthetrum albistylum speciosum	1	86	○	○	-	-	-	-
Ischnura senegalensis	2	55	○	○	-	-	-	-
Pantala flavescens	3	66	○	○	-	-	-	-
Mnais pruinosa	4	62	+	-	-	-	-	-
Anax parthenope julius	5	57	○	○	-	-	-	-
Copera annulata	6	47	○	-	-	-	-	-
Calopteryx cornelia	7	49	-	-	-	-	-	○
Sympetrum frequens	8	47	○	-	-	-	-	-
Asiagomphus melaenops	9	49	○	-	-	-	-	-
Gynacantha japonica	10	34	○	-	-	-	-	-
Anotogaster sieboldii	11	53	○	-	-	-	-	-
Calopteryx atrata	12	45	+	+	-	-	-	-
Crocothemis servilia mariannae	13	47	○	○	-	-	-	-
Cercion calamorum calamorum	14	50	○	○	-	-	-	-
Orthetrum triangulare melania	15	46	○	-	-	-	-	-
Lyriothemis pachygastra	16	41	○	○	-	-	-	-
Rhipidolestes aculeatus yakushimensis	17	23	-	-	-	-	-	○
Orthetrum japonicum japonicum	18	42	○	○	-	-	-	-
Sympetrum eroticum eroticum	19	42	○	-	-	-	-	-
Sympetrum darwinianum	20	39	○	-	-	-	-	-
Davidius nanus	21	30	○	-	-	-	-	-
Sieboldius albardae	22	33	○	+	-	-	-	-
Epiophlebia superstes	23	21	-	-	-	-	-	○
Pseudothemis zonata	24	39	○	-	-	-	-	-
Macromia amphigena amphigena	25	25	○	-	-	-	-	-
Lanthus fujiacus	26	23	-	-	-	-	-	○
Sympetrum speciosum speciosum	27	30	○	-	-	-	-	-
Anax nigrofasciatus nigrofasciatus	28	35	○	-	-	-	-	-
Indolestes peregrinus	29	31	○	-	-	-	-	-
Planaeschna milnei	30	34	+	-	-	-	-	○
Stylogomphus suzukii	31	21	-	-	-	-	-	-
Sympetrum parvulum	32	33	+	-	-	-	-	-
Sympetrum pedemontanum elatum	33	27	-	-	-	NT	-	-
Somatochlora uchidai	34	27	○	-	-	-	-	-
Sympetrum risi risi	35	25	○	-	-	-	-	-
Aciagrion migratum	36	22	○	-	-	-	-	-
Ceriagrion melanurum	37	27	○	-	-	-	-	-
Calopteryx japonica	38	20	-	-	-	NT	-	○
Epophthalmia elegans	39	24	○	○	-	-	-	-
Rhyothemis fuliginosa	40	24	+	-	-	-	-	-
Libellula quadrimaculata asahinai	41	27	○	+	-	-	-	-
Trigomphus citimus tabei	42	24	○	-	-	-	-	-
Polycanthagyna melanictera	43	19	○	-	-	-	-	-
Lestes temporalis	44	22	○	-	-	-	-	-
Sympetrum kunckeli	45	15	-	-	-	VU	-	-
Sympetrum striolatum imitoides	46	13	-	-	-	-	-	-
Sympetrum baccha matutinum	47	19	○	-	-	-	-	-
Ischnura asiatica	48	19	○	○	-	-	-	-
Anaciaeschna martini	49	19	○	-	-	-	-	-
Sympetrum infuscatum	50	15	○	-	-	-	-	-
Deielia phaon	51	15	○	○	-	-	-	-
Ceriagrion nipponicum	52	20	○	-	VU	-	-	-
Boyeria maclachlani	53	12	-	-	-	-	-	-

continued

continued

Lestes sponsa	54	17	O	-	-	-	-	-
Tanypteryx pryeri	55	11	-	-	-	NT	-	O
Anisogomphus maacki	56	14	-	-	-	-	-	O
Platycnemis foliacea sasakii	57	14	O	-	VU	NT	-	-
Epitheca marginata	58	16	-	-	-	-	-	-
Sinogomphus flavolimbatus	59	9	-	-	-	-	-	O
Sympetrum croceolum	60	15	+	-	-	-	-	-
Mnais costalis	61	10	-	-	-	-	-	-
Cercion hieroglyphicum	62	18	O	O	-	-	-	-
Trigomphus interruptus	63	15	+	-	-	-	-	-
Asiagomphus pryeri	64	12	-	-	-	-	-	-
Ictinogomphus pertinax	65	14	-	-	-	-	O	-
Oligoaeschna pryeri	66	14	O	-	-	NT	-	-
Trigomphus ogumai	67	13	-	-	-	-	-	-
Nihonogomphus viridis	68	13	-	-	-	NT	-	-
Gomphus postocularis	69	8	-	-	-	NT	-	-
Sinictinogomphus clavatus	70	15	O	-	-	-	-	-
Aeschnophlebia longistigma	71	12	-	-	-	-	-	-
Davidius fujiama	72	9	-	-	-	-	-	O
Sympecma paedisca	73	8	-	-	-	-	O	-
Cercion sexlineatum	74	8	-	-	-	NT	-	-
Tramea virginia	75	8	+	+	-	-	O	-
Onychogomphus viridicosta	76	11	-	-	-	-	-	O
Mortonagrion selenion	77	7	-	-	-	VU	-	-
Aeschnophlebia anisoptera	78	6	+	-	-	NT	-	-
Agriocnemis femina oryzae	79	5	-	-	-	-	-	-
Cercion sieboldii	80	5	-	-	-	-	-	-
Aeschna nigroflava	81	4	-	-	-	-	-	-
Somatochlora clavata	82	4	-	-	-	-	O	-
Orthetrum sabina sabina	83	4	-	-	-	-	O	-
Lestes japonicus	84	7	-	-	VU	-	-	-
Macromia daimoji	85	3	-	-	VU	VU	-	O
Nannophya pygmaea	86	3	-	-	-	VU	-	-
Sympetrum uniforme	87	3	-	-	VU	-	-	-
Somatochlora viridiaenea viridiaenea	88	2	-	-	-	-	O	-
Stylurus nagoyanus	89	2	-	-	-	-	-	O
Anax guttatus	90	1	-	+	-	-	O	-
Tholymis tillarga	91	1	-	-	-	-	O	-
Total		91	52	17	4	13	8	13

Chapter 6 General Discussion and Conclusions

In the face of the rapid biodiversity loss, biodiversity conservation is becoming an international urgent issue. Agricultural ecosystem is one of terrestrial areas where the biodiversity have lost most rapidly (Ormerod *et al.* 2003). In order to prevent the loss of biodiversity, it is emergently needed to monitor the biodiversity to acknowledge the accurate current status of biodiversity and to evaluate the consequence of conservation efforts.

Trends in the abundance and distribution of population of indicator species is what most biodiversity monitoring has been focused (Balmford *et al.* 2005). However, survey work to monitor the species' status directly at larger spatial scale can be very expensive and sometimes not feasible. Therefore, the monitoring is often directed not at the population itself, but at their abiotic or biotic environments determined or assumed to be important to the species, and through modeling the relationships between these habitat variables and the distribution of target species (Rushton *et al.* 2004).

With the rise of new powerful statistical techniques and GIS tools, the development of predictive habitat distribution models has rapidly increased in ecology (Rushton *et al.* 2004). In spite of the rapid development of methodology for modeling to predict the distribution of organisms, most of models are generally built with few or no attention to spatial processes which are dependent or operate across different spatial scales (Guisan & Zimmermann 2000). Recently, importance of such ecological processes appear necessary to explain the patterns

of distribution, abundance and interaction of organisms at local as well as regional scales (Hanski & Glipin 1997; Leibold *et al.* 2004; Rietkerk *et al.* 2004).

Immigration potential of individuals, which is defined as 'expected ease of colonization' to a habitat for individuals, has been revealed to determine the proneness to extinction of local populations, and consequently has significant effects on metapopulation viability (Hanski 1999; Vos *et al.* 2001). Immigration potential of species also plays an important role in determining the species diversity at local communities (Cadotte 2006; MacArthur & Wilson 1967) and metacommunity dynamics (Koelle & Vandermeer 2005). Therefore, the distribution and magnitude of immigration potential at landscape scale would be one of fundamental measures to monitor the dynamics of population and communities, or to predict the recovery potential of species in a restored habitat.

In the present thesis, dragonflies in agricultural and freshwater habitat complex as a case study, I aimed to answer following questions to: (1) what factors do determine abundance and species richness at local habitat scale; (2) what factors do determine the immigration potential of individuals at landscape scale and (3) what factors do determine the immigration potential of species to newly restored habitat. These questions would be fundamentally related to a general question, that is, how biodiversity can be monitored with 'dragonfly' as an indicator. I addressed these questions using 'spatial ecological approach' in which spatial ecological processes are explicitly considered as explained in Chapter 1.

In order to estimate the immigration potential of dragonfly individuals, it was needed to observe the frequency of immigration to habitats of which initial condition has been known. Therefore in Chapter 2 and 3, I analyzed the data on

the abundance of multiple dragonfly species at a number of small ponds newly created around Lake Kasumigaura in Ibaraki Pref. in eastern Japan. At the beginning, I revealed that observed species richness and abundance at the ponds were influenced by local habitat characteristics (i.e., pond surface area and vegetation cover) (Chapter 2). In Chapter 3, in order to examine the relationships between spatial arrangement of habitat patches around ponds and abundance of dragonfly individuals at the ponds, I employed two approaches for analysis: one is to model the dispersal process explicitly using exponential-decline kernel (Rhodes *et al.* 2006) and the other is to quantify the extent and magnitude of spatial autocorrelation using variation partitioning analysis coupled with trend surface analysis (Legendre & Legendre 1998). From the result of the analyses, it was indicated that landscape structure around the ponds and species life history characteristics (i.e., long v.s. short pre-reproductive phase) are interacting to determine the abundance of dragonfly species at the sampling ponds as well as the local pond characteristics.

To further clarify the effects of interaction between landscape structure and the species life history characteristics on immigration potential of individuals at landscape scale, I employed bottom-up modeling approach and developed spatially explicit individual-based simulation model coupled with realistic landscape structure and the life history characteristics of individuals (Chapter 4). Because information about habitat types or ecological characteristics of dragonflies have been well documented (e.g., Sugimura *et al.* 1999), the approach which can incorporate these knowledge flexibly into a model would be suitable to construct an effective prediction model for immigration potential of dragonfly

individuals. In addition, in order to reduce the uncertainty and estimate reliable model parameters, I employed pattern-oriented modeling approach (Wiegand *et al.* 2003) and estimated the model parameters indirectly by comparing the model predictions with the observed pattern of dragonfly immigration to the newly created ponds systematically.

Using the model, I quantitatively analyzed the response of immigration potential to the spatial arrangement of habitat patches at landscapes. From the prediction of the model, it was indicated that immigration potential of longer pre-reproductive phase species linearly increased according to increasing the amount of available woodland habitats on a landscape where adequate aquatic habitats were available. On the other hand, their response to the increasing of the woodland became nonlinear when the aquatic habitats were deficient or distributed separately form the woodland habitats.

In Chapter 5, in order to predict the immigration potential of species, I used a national database of wildlife record, and estimated the immigration potential of each dragonfly species from the relative prevalence of each species at eco-regional scale. It was demonstrated that the order of species recovery at the restoration site roughly followed the predicted immigration potential of each species. Based of these result, I proposed a handy procedure for prediction the trajectory of species re-establishing themselves in a newly restored habitat by comparing the estimated nested species pool and the observed current state of species recovery at the target site. Considering the species pool explicitly to predict the trajectory of species recovery, the procedure is applicable to any local communities having a regionally nested species pool.

With these studies, I elucidated that spatial processes play an important role in determining the immigration potential of dragonflies. Spatial arrangement of habitat patches and habitat use pattern of species were shown to interact to determine the immigration potential of individuals at landscape scale. On the other hand, species prevalence at an eco-regional scale was indicated to affect the immigration potential of species at the local restoration site.

Restoration projects as experiments at landscape scale

In order to investigate regional effects on local populations or communities, it would be desirable to examine many replicate sets of patches, varying in the type of matrix habitat, the presence or absence of corridors, or the distance among patches. However, sets of many similar habitat fragments area hard to find. Not only fragment size and shape, but history, habitat type, proximity to human disturbances, and many other features may vary even within a single region. Therefore it is not surprising that there have been few studies that empirically examine the effects of landscape fragmentation at realistic larger spatial scale (Harrison & Bruna 1999).

In the present thesis I conducted field surveys at freshwater habitats simultaneously created by regional restoration projects in Japan and observed the frequency of immigration to habitats of which initial condition has been known. A number of, or spatially larger aquatic habitats which were newly created in the projects have provided me good opportunities to examine the questions in the studies experimentally (Chapters 2, 3 & 4), or to validate model predictions at realistically larger spatial scale (Chapter 5) which is quite difficult to be

conducted on an individual based.

As demonstrated in the present thesis, habitat modifications are operated on a larger spatial scale than as usual for conservation and management purposes can provide invaluable opportunities for ecological experiments on a large scale.

The implementation of such experiments would be also of benefit to the ecological success of the project, if the hypotheses tested in the experiments are relevant to the purpose of the projects, because the appropriate management experiments with appropriate control and replication is one of key elements in the process of adaptive management (Walters 1997) and they would tell the objective consequence of the conducted management operations and the next directions to which the project should be improved.

Effects of species' ecological characteristics on connectivity

From the animal's perspective, fragmented landscapes may differ from non-fragmented ones in both the composition and configuration of habitat patches (Dunning *et al.* 1992). The degree to which connectivity (Taylor *et al.* 1993) differs among landscapes depends on how animals perceive, utilize, and move through the various habitat patches and how these patches are configured. These decisions by animals on dispersal responses, in turn, affect how individuals are distributed over landscapes. For dragonflies, Jonsen & Taylor (2000) demonstrated that in transplant experiments of two congeneric species – *Calopteryx aequabilis* and *C. maculate*, both species moved away from the streams where they were introduced on landscape with high or moderate levels of forest cover but neither move away from streams on landscapes with little or no

forest. It was also shown that *C. maculata* native to predominantly forested landscapes are more likely to move away from streams, regardless of the forested or non-forested landscapes, whereas there was no effect of natal landscape on *C. aequabilis*.

In Chapters 3 and 4, it was demonstrated that the sensitivity to spatial distribution of woodland patches differed between long and short-phase species which are known to utilize the habitat differently. These facts indicated that in order to predict the immigration potential of dragonflies, it is critical to consider multiple habitat types they use and how they use these habitats, which can be mutually distant in the currently fragmented landscapes.

There are many animals which have complex life cycles (Wilbur 1980) and change the habitat type according to life stages including aquatic insects and amphibians as well as dragonflies in the present study. To construct a reliable model for prediction of immigration potential for such animals and their distributions over landscapes, it would be needed to incorporate the biological details (i.e., how they use the multiple habitat types according to their life stages) into the model.

Dispersal as a key process to predict the immigration potential

Although most of the distribution models are static and probabilistic in nature (Guisan & Zimmermann 2000), distribution pattern of organisms is not static but apparently composite results of dynamic processes including dispersal and biological interactions as well as environmental constraints (e.g., Buckley & Roughgarden 2005), and thus when such dynamic processes play important roles

in determining the distribution, a mechanistic model would be needed based on real cause–effect relationships to make a credible prediction of the distribution. From the results of Chapter 3 and 4, it was demonstrated that dispersal was one of fundamental processes affecting the immigration potential of individuals at landscape scale.

Several techniques have been proposed to incorporate the dispersal process into a distribution model as mentioned in Chapter 1. Among them, spatially explicit simulation approach may provide us powerful tools to capture the essentials of the dispersal process and dynamics of the population(s), and frequently used in conservation studies (Beissinger & McCullough 2002). However, the spatially explicit population models have been heavily criticized for needing an excessive amount of biological data. Especially, estimation of parameters regarding dispersal survival and success is difficult, and, as dispersal success is an important parameter in many populations, spatially explicit models of these populations may be prone to error propagation (Ruckelshaus *et al.* 1997).

However, Mooij & DeAngelis (2003) demonstrated that spatially explicit dispersal models that include relevant landscape details does not necessarily increase uncertainty and may be preferable over simpler models that ignore basic information on the system at hand, even in cases where specific field data are scarce. The recent progress in model development and theory allows better parameter estimation in spatially explicit population models. One of such approaches is to extract information from population patterns in space, which can help refine parameter estimates (pattern-oriented modeling sensu Wiegand *et al.* 2003), which has been used in Chapter 4. It seems reasonable to suppose that

judicious employment of landscape details, movement strategies, and the available field data on dispersal enable spatially explicit models to serve as important and reliable tools to predict immigration potential and dynamics of populations.

Dispersal links the local communities or connects sink communities with source ones, and is also recognized as a key ecological process to determine the immigration potential of species and the species richness at local communities (Cadotte 2006; MacArthur & Wilson 1967). In Chapter 5, I could propose a general procedure to predict the trajectory of species recovery, based on the consideration of species immigration from the regional species pool. Such a prediction method is applicable to any local community having a regionally nested species pool.

Dragonflies and spatial ecological approach for biodiversity monitoring

The loss of semi-natural habitats due to agricultural intensification and marginalization of traditional agricultural systems, both of which have led to the abandonment of tradition land use, is one of the main threats to biodiversity in agricultural ecosystems (Krebs *et al.* 1999; Ormerod *et al.* 2003). In east Asia including Japan, Odonata is one of the major taxa depending on the agricultural habitat complex maintained by the traditional land use, and have been widely proposed as indicator of the ecological quality of land–water ecotones, aquatic habitat heterogeneity (e.g., bank morphology and aquatic vegetation), and the hydrological dynamics of water bodies (e.g., Chovanec & Waringer 2001; Clark & Samways 1996; D'Amico *et al.* 2004).

In Chapter 4, I constructed a dispersal model using the pattern-oriented modeling approach. Because the model was parameterized by systematic comparisons of its predictions with the observed patterns, I could say that the model predictions had been partly validated. The predictions of the model using the selected parameter sets were reasonably understood by the model assumptions and spatial arrangement of habitat patches at the landscapes, and the model was indicated to perform well. Therefore, the model would be applicable as a tool for prediction and monitoring of immigration potential of dragonfly individuals at the landscapes in the present study.

In Chapter 5, it was demonstrated that the trajectory of species recovery followed the estimated species immigration potential at the regional scale. From another point of view, immigration potential of dragonfly species at an eco-regional scale could be evaluated from the recovery trajectory of species in habitat restoration sites where restoration projects have been newly implemented. Although the site used for the monitoring should have adequate site capacity for inhabitation of a number of dragonfly species, projects of wetland restoration implemented on a large scale is increasing in number recently (Yoshimura *et al.* 2005). Adopting the procedure proposed in Chapter 5 at these wetland restoration projects implemented in various eco-regions, it would become possible to monitor the immigration potential of dragonfly species at whole country scale.

The biodiversity monitoring requires a series of standardized, regularly repeated measurements of the state of biomes and their biota. These measurements must capture various invaluable information on the biomes concerned; the diversity, distribution, and abundance of species (e.g., Ceballos &

Ehrlich 2002). The methodology for modeling to predict the distribution of various organisms including both plants and animals had been developed rapidly (Guisan & Zimmermann 2000; Rushton *et al.* 2004). In addition, recently, spatial ecological processes have been recognized as important determinants of biographical patterns of species distributions (Gaston 2003). Spatial ecological approach taking into account such ecological spatial processes, including treatment of spatial autocorrelation, consideration of organisms' dispersal, complex responses to landscape structure and species pool as a case in the present thesis, therefore, would be valuable to improve the precision of model predictions and to enable effective monitoring for biodiversity conservation.

Problems left to be explored

Biological interactions such as predation and competition, which I did not consider in the present thesis, may play certain important roles in determining the distributional patterns and regional community structure of dragonflies. In general, it is predicted theoretically that species interaction can occur in a network of local communities where they affect colonization probabilities and extinction patterns at a larger scale (Koelle & Vandermeer 2005). Dragonfly larvae were predators in aquatic systems, and presence/absence or abundance of them were reported to drastically alter community structures (Kadoya & Washitani in preparation) and ecosystem functions (Ngai & Srivastava 2006) in aquatic systems through top-down effects. In addition, among dragonfly species, smaller species were sensitive to predation by co-occurring larger species (Kadoya & Washitani in preparation). Therefore, in some situations, there are possibilities that the

immigration potential of larger (i.e., top predators) or superior competitor species and spatial factors which determine connectivity for them affect the distributional pattern of the smaller-sized (i.e., preys) or inferior competitor species.

From a methodological point of view, the development of techniques appropriately dealing with various sources of uncertainties that are inevitably contained in data collected from large spatial scale or assembled from different data sources would be needed. In order to capture the species distribution at larger spatial scale, such as regional, a dynamic cycle with feedback loops between data collection and model prediction would be needed to increase reliability of model structures and predictions. Data collected from the larger spatial scale or from different existing databases inevitably suffer from practical complications relating to sampling, including observer error, variable sampling intensity and gaps in sampling, or a spatial mismatch between different data sources. Development of a modeling framework addressing these problems would be critically important for prediction of species distribution at larger spatial scale. Possibly, Bayesian framework would provide a powerful tool to address such problems (Latimer *et al.* 2006).

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