

Niche dynamics of species in succession process in the Wetland of Yangtze Rivers Lower Reach, China

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Background and aims – The niche theory has become one of the fundamental theories to explain species coexistence. In the present study, the relationships between competition/ facilitation and species niche, and between displacement /coexistence and species niche were further explored by studying the realized niche dynamics of species along a succession process.

Materials and methods – By using space series to replace time courses, the niche dynamics of species involved in the plant community succession process in the Waterfront Wetland of Yangtze Rivers Lower Reach, China, were studied by using the formula described by Levins and Pianka.

Key results – Results showed that every succession stage community was dominated by the species with the highest or/and second highest niche breadths, revealing that these species had broader environmental tolerances and were able to use a wider range of resources. In general, niche overlaps were greater among species with higher niche breadths. The total average niche overlaps of all paired species at different succession stages first increased, reached its maximum in the late-middle stage, and then finally decreased slightly in the late stage in the entire succession process.

Conclusion – The dynamic characteristics of niche of species reflect the process of displacement of species along the community succession process. The higher niche overlaps reflect the instability and transition state of plant communities along the successional process. Facilitation, as well as competition, occurs in the different species with higher niche overlap.

Key words – Niche breadth, niche overlap, succession process, competition, facilitation.

INTRODUCTION

The niche concept, initially conceived by the zoologist Joseph Grinnell (Grinnell 1917), emphasized the role of habitat and food in defining the niche of an animal (Chase & Leibold 2003). Hutchinson took this definition one step further by suggesting a quantitative formulation of the niche (Hutchinson 1957) and further distinguished between the fundamental niche of a species as an n-dimensional hypervolume, which is genetically and physiologically determined, and the realized niche, which includes, additionally, constraints arising from interspecific competition, and pointed out that the fundamental niche of one species may shrink to a smaller realized niche in the presence of other species (Pearman et al. 2007). Both Hutchinson's and Grinnell's niche concepts focus on an organism's response to abiotic and biotic environmental constraints (Kylafis & Loreau 2011). The niche concept, since its inception, has actually been controversial (Kylafis & Loreau 2011), but some of the confusion over the niche concept can be clarified by keeping in mind that all

species not only respond to variation in the environment, but they also all change the environments in which they occur (Pulliam 2000). The niche theory has become one of the fundamental theories to explain species coexistence and competition in natural plant communities (Shugart et al. 1988, Silvertown 2004, Kelly & Bowler 2009). Niche involves two complementary aspects: one relates to the space occupied by a group of species or a community in the ecological space and the other relates to resource utilization and competition among coexisting species (Lakkis 1994). They may be well illuminated by two important niche indices, namely niche breadth and niche overlap (Decaëns et al. 2011, Kovács & Carroll 2010, Mutshinda & O'Hara 2011). Niche breadth measures the range of resource characteristics across which a species exists, and indicates the extent that species utilize different types of resources. Niche overlap has often been used as a measure of potential competition between species (Milne & Mason 1990). In recent years, studies of niche breadth and overlap in plant communities have tended to focus on the physiology and growth form of plants as the

main determinants of niche structure and species coexistence (Silvertown et al. 2001, Chase & Leibold 2003, Silvertown 2004, Ollerton et al. 2007). In recent years, research on niche dynamics of species in community succession processes or at evolutionary level have been reported, such as niche dynamics of main populations of plants communities in the restoring succession process in sandy land (Zhang et al 2003) and niche dynamics of earthworms in an aging pasture gradient (Dacaëns et al. 2011). In the present study, the realized niche dynamics of species along a plant community succession process in Zhenjiang Waterfront Wetland was studied. This research together with the two ones above-cited were all conducted along environmental gradients, so it will reveal well the feedback between plants and environments and plants' responses to changing environments, and further explore the relationships between competition/facilitation and species niche, and between displacement/coexistence and species niche along a succession process.

MATERIALS AND METHODS

Study site

Zhenjiang City is located on the southern shore of the Yangtze River (32°15'N and 119°28'E). The Zhenjiang Waterfront Wetland, a 5000-hectare intermittent river wetland, lies to the north of Zhenjiang City along the Yangtze River (fig. 1), and was formed from the accumulation of massive silt deposits in the Yangtze River water. About 3–4 years after mudflats without vegetation developed due to sediment accumulation, the primary succession of the plant community gradually began with the emergence and expansion of *Phalaris arundinacea*, which acted as the pioneer species and subsequently became the mono-dominant population in the community until about 10–12 years after mudflats without vegetation developed. Upon further elevation of the river beach and the establishment and expansion of *Phragmites communis* over time, *Phragmites communis* and *Phalaris arundinacea* constituted the co-dominant populations in the community until nearly 24–27 years after the mudflats devel-

oped. As time passed, the *Phalaris arundinacea* population gradually declined, while the *Phragmites communis* population continuously expanded. Ultimately, *Phragmites communis* became the mono-dominant population, while *Phalaris arundinacea* was transformed into a companion species until nearly 35 years after mudflats developed (Fu et al. 2011). The plant community had passed through three community types over its succession process, namely, initial *Phalaris arundinacea* community, intermediate *Phalaris arundinacea-Phragmites communis* community, and climax *Phragmites communis* community.

Nomenclature

The names of taxa follow nomenclature from *Iconographia Cormophytorum Sinicorum* (Institute of Botany, Chinese Academy of Sciences 1972a, 1972b, 1974, 1975).

Sampling methods

Four typical sample plots were chosen within the study site in the end of April, when plants in the Zhenjiang Waterfront Wetland were in most abundance, by using space series to replace time courses based on data on the evolution of a plant community provided by the Zhenjiang Beach Administrative Bureau. These plots represented four different succession stages within the study site, namely Stage I (Initial stage), Stage II (Early-middle stage), Stage III (Late-middle stage), and Stage IV (Late stage) (table 1). We set 40 quadrats (2 × 2 m) on the diagonal line within every sample plot where plant species were identified, counted, and measured for coverage, height, density, and frequency. In total, data were collected from 160 quadrats in the study site.

Data analysis methods

In the present study, each quadrat was regarded as a synthetic resource station that included multi-dimension resources, and the number of quadrats was that of resource gradients (Colwell & Futuyma 1971, Hu et al. 2006). The niche



Figure 1 – Location of Zhenjiang and the Zhenjiang Waterfront Wetland in China.

Table 1 – Characteristics of different type sample plots.

| Succession stage | Succession time/a | Elevation of sample plots/m | Dominant species |
|------------------|-------------------|-----------------------------|--|
| Stage I | 3–5 | 2.8–2.9 | <i>Phalaris arundinacea</i> |
| Stage II | 10–12 | 3.0–3.1 | <i>Phalaris arundinacea</i> |
| Stage III | 24–27 | 3.6–3.7 | <i>Phragmites communis</i> - <i>Phalaris arundinacea</i> |
| Stage IV | about 35 | 4.4–4.5 | <i>Phragmites communis</i> |

breadths of species and the niche overlaps among species were calculated using the relative importance value index, which was expressed as the sum of relative density, relative coverage, relative height, and relative frequency divided by four to eliminate errors caused by individual difference (Hu et al. 2006).

The niche breadth of species is an estimate reflecting the diversity of environmental resource-use and the ecological amplitude of species. The Simpson formula, Shannon-Weiner formula, and Levins formula are the most commonly used methods to calculate the niche breadth of species, of which Levins formula is a combination of the other two formulae, and can more directly reflect the size of the niche breadth of plant population and facilitate comparison of niche breadth among different species (Zhou et al. 1999). The approach proposed here is the formula described by Levins (1968), which was defined as

$$BL_i = 1 / (r \sum p_{ij}^2), j = 1, 2, \dots, r$$

where BL_i is the niche breadth of species i and ranges from $1/r$ (use of a single resource) to 1 (equal usage of all resources available); and r is the number of resource gradients available. The term p_{ij} is the proportion of species i using resource gradient j to the total resources available, and is calculated from

$$p_{ij} = n_{ij} / N_i, N_i = \sum n_{ij}, j = 1, \dots, r$$

in which n_{ij} is the relative importance value of species i in the resource gradient j . In the present study, r is the number of quadrats.

If each sere is regarded as a multi-dimensional space with various plant community types at different succession stages, the total niche breadth of species (BL_i) in the entire sere is calculated by using the formula

$$BL_i = (\sum BL_j^2)^{1/2}, j = 1, 2, \dots, m$$

where BL_j indicates the Levins niche breadth of species in the succession stage j or the community type j ; and m is the number of community succession stage or community type within the entire succession process (Li et al. 1995, Hu et al. 2006). In the present study, m was 4, indicating that the entire succession process included four different succession stages.

The niche overlap reflects the degree of similarity of different species for environmental resource demands. It has of-

ten been used as a measure of potential competition between species and is calculated as Pianka niche overlap formula

$$O_{ik} = \sum n_{ij} n_{kj} / (\sum n_{ij}^2 \sum n_{kj})^{1/2}, j = 1, \dots, r$$

where O_{ik} is the niche overlap between species i and species k and ranges from 0 (no overlap) to 1 (full overlap). Similarly, r is the number of quadrats, and n_{ij} and n_{kj} are the importance values of species i and species k , respectively (Pianka 1973).

The above niche breadth and niche overlap were based on the relative importance value obtained from the field community survey, which indicate the actual niche possession of species (Zhang et al. 2003, Hu et al. 2006). Therefore, niche in the present study is regarded as the realized niche, and can reflect well the relationships between competition, facilitation, coexistence, and niche in the wetland plant community.

RESULTS

The niche breadth

Tables 1 & 2 demonstrate that at the Initial stage (Stage I), the elevation of river beach in the wetland was the lowest. Species were rare with only four present, of which the niche breadth of *P. arundinacea*, a pioneer species, was the highest (0.5142) and much larger than that of the other three species, *Alopecurus aequalis*, *Potamogeton distinctus*, and *Potamogeton crispus*, which indicated that *Phalaris arundinacea* was the mono-dominant species in the community and was able to survive in more places or over a larger area. At Stage II, the Early-middle stage, besides all the four species at the previous stage, ten new species established and occupied a certain niche, respectively. The niche breadth of *Phalaris arundinacea* increased and remained as the highest (0.6243) at this stage, and was also much higher than that of *Cardamine yrata* (0.3606), the second highest at this stage. All these showed that *Phalaris arundinacea* was still the mono-dominant species in Stage II community. With succession into Stage III, the Late-middle stage, the number of species in the community had reached a maximum of 33, more than in any other stage communities, which would inevitably lead to fierce interspecific competition and niche-reformation of species under limited environmental conditions. Although still highest, the niche breadth of *Phalaris arundinacea* declined to 67.6% of that at Stage II. The niche breadths of the other two species, *Phragmites communis* and

Table 2 – The niche breadths of species at different succession stages.

| Species | Niche breadth of species at different succession stages | | | | Total niche breadth of species |
|------------------------------------|---|----------|-----------|----------|--------------------------------|
| | Stage I | Stage II | Stage III | Stage IV | |
| <i>Phalaris arundinacea</i> | 0.5142 | 0.6243 | 0.4223 | 0.2871 | 0.9565 |
| <i>Alopecurus aequalis</i> | 0.2052 | 0.2254 | 0.2502 | 0.1043 | 0.4079 |
| <i>Potamogeton distinctus</i> | 0.1235 | 0.0938 | - | - | 0.1551 |
| <i>Potamogeton crispus</i> | 0.1831 | 0.1013 | 0.0324 | - | 0.2117 |
| <i>Cardamine yrata</i> | - | 0.3606 | 0.2524 | 0.1014 | 0.4517 |
| <i>Limnophila sessiliflora</i> | - | 0.2013 | - | - | 0.2013 |
| <i>Ranunculus sceleratus</i> | - | 0.3068 | 0.2134 | 0.0972 | 0.3862 |
| <i>Polygonum hydropiper</i> | - | 0.1032 | 0.1001 | 0.0921 | 0.1707 |
| <i>Zizania caduciflora</i> | - | 0.4321 | 0.3224 | - | 0.5391 |
| <i>Oenanthe decumbens</i> | - | 0.2431 | 0.1243 | 0.2212 | 0.3514 |
| <i>Alternanthera philoxeroides</i> | - | 0.2113 | 0.1864 | - | 0.2818 |
| <i>Hydrocharis dubia</i> | - | 0.0754 | - | - | 0.0754 |
| <i>Polygonum lapathifolium</i> | - | 0.3421 | 0.3989 | - | 0.5255 |
| <i>Artemisia selengensis</i> | - | 0.2315 | 0.1218 | 0.1345 | 0.2941 |
| <i>Phragmites communis</i> | - | - | 0.4057 | 0.6743 | 0.7869 |
| <i>Polygonum perfoliatum</i> | - | - | 0.0842 | 0.0857 | 0.1201 |
| <i>Cardamine hirsuta</i> | - | - | 0.1325 | - | 0.1325 |
| <i>Rumex japonicus</i> | - | - | 0.1017 | - | 0.1017 |
| <i>Daucus carota</i> | - | - | 0.1942 | 0.1124 | 0.2244 |
| <i>Aster tataricus</i> | - | - | 0.0564 | 0.1547 | 0.1647 |
| <i>Veronica aquatica</i> | - | - | 0.1021 | - | 0.1021 |
| <i>Beckmannia syzigachne</i> | - | - | 0.2758 | - | 0.2758 |
| <i>Trigonotis peduncularis</i> | - | - | 0.0042 | - | 0.0042 |
| <i>Rorippa islandica</i> | - | - | 0.2852 | 0.0942 | 0.3004 |
| <i>Chenopodium album</i> | - | - | 0.0073 | 0.1458 | 0.1406 |
| <i>Potentilla chinensis</i> | - | - | 0.0074 | - | 0.0074 |
| <i>Actinostemma lobatum</i> | - | - | 0.1987 | 0.2143 | 0.2922 |
| <i>Kalimeris indica</i> | - | - | 0.0945 | 0.3421 | 0.3549 |
| <i>Cardamine flexuosa</i> | - | - | 0.1326 | 0.2117 | 0.2498 |
| <i>Rumex dentatus</i> | - | - | 0.0997 | 0 | 0.0997 |
| <i>Salvia japonica</i> | - | - | 0.0942 | 0.1073 | 0.1428 |
| <i>Potentilla supina</i> | - | - | 0.0958 | - | 0.0958 |
| <i>Carex cinerascens</i> | - | - | 0.0872 | 0.3672 | 0.3774 |
| <i>Sclerochloa kengiana</i> | - | - | 0.1051 | - | 0.1051 |
| <i>Rorippa indica</i> | - | - | 0.0543 | - | 0.0543 |
| <i>Capsella pastoris</i> | - | - | 0.1045 | 0.0721 | 0.1270 |
| <i>Hemistepta lyrata</i> | - | - | 0.1012 | 0.2357 | 0.2565 |
| <i>Calystegia hederacea</i> | - | - | - | 0.2873 | 0.2873 |
| <i>Humulus scandens</i> | - | - | - | 0.0879 | 0.0879 |
| <i>Paederia scandens</i> | - | - | - | 0.1942 | 0.1942 |
| <i>Mazus stachydifolium</i> | - | - | - | 0.1012 | 0.1012 |
| <i>Conyza canadensis</i> | - | - | - | 0.0735 | 0.0735 |
| <i>Vicia angustifolia</i> | - | - | - | 0.1527 | 0.1527 |
| <i>Miscanthus sacchariflorus</i> | - | - | - | 0.2874 | 0.2874 |

Polygonum lapathifolium, were 96.1% and 92.1% that of *Phalaris arundinacea*, respectively. The dominant status of *Phalaris arundinacea* was greatly weakened. *Phalaris arundinacea* was no longer the mono-dominant species but rather the co-dominant species together with *Phragmites communis* and/or *Polygonum lapathifolium* in the Stage III community. With succession into Stage IV, the Late stage, the number of species decreased to 27. The niche breadth of *Phalaris arundinacea* decreased to 0.2872. In contrast, the niche breadth of *Phragmites communis* extended sharply to 0.6743 and became 134.8% larger than that of *Phalaris arundinacea*. It was also 83.6% larger than that of *Carex cinerascens*. Another potential dominant species, *Polygonum lapathifolium* at Stage III, completely disappeared at Stage IV. The results above show that both *Phalaris arundinacea* and *Polygonum lapathifolium* were no longer the co-dominant species, while *Phragmites communis* had developed to be the mono-dominant species in the Stage IV community.

Table 2 shows that niche breadths of some hydrophytes such as *Potamogeton distinctus*, *Potamogeton crispus*, and *Limnophila sessiliflora* at Stage II, and some phreatophytes, such as *Zizania caduciflora*, *Cardamine yrata*, and *Ranunculus sceleratus* at Stage III, decreased, whereas that of some terrestrial vegetation, such as *Kalimeris indica* and *Carex cinerascens* at Stage III, increased compared to the previous succession stage. These findings were consistent with the fact that the environmental conditions on the river beach gradually presented an evolutionary trend from aquatic to terrestrial with the elevation of river beach across the entire succession process. The species that adapting to the corresponding habitats broadened their niches, whereas other species non adapting to their corresponding habitats gradually narrowed their niches. These results demonstrate the co-evolutionary relationship between plants and environmental conditions from the aspects of niche.

As shown in table 2, the total niche breadth of *Phalaris arundinacea* was 0.9565, larger than that of any other species, and that of *Phragmites communis* was second highest with 0.7869. This was consistent with their dominant species status at one or two succession stages. These were followed by *Zizania caduciflora*, *Polygonum lapathifolium*, and *Cardamine yrata*, which appeared at two or three succession stages. This was consistent with their companion species status across the entire succession process. Other species, such as *Trigonotis peduncularis* and *Potentilla chinensis*, were only present at a particular stage with much lower niche breadths. This showed their extraordinary low ability to adapt to the environment and was consistent with their rare species status across the entire succession process.

The niche overlap

Table 3 shows that a relatively lower niche overlap among species occurred at Stage I, obviously because species were rare and the resources were relatively adequate for these species, so every species could independently utilize environmental resources at this stage. The niche overlap between *Phalaris arundinacea* and *Alopecurus aequalis* was highest, which expressed the high ecological similarity of these two species. Despite the lower niche breadths of *Potamogeton*

Table 3 – The niche overlaps of species at Stage I along the succession process.

| Species | 1 | 2 | 3 | 4 |
|---------------------------------|------|------|------|---|
| 1 <i>Phalaris arundinacea</i> | 1 | | | |
| 2 <i>Alopecurus aequalis</i> | 0.38 | 1 | | |
| 3 <i>Potamogeton distinctus</i> | 0.14 | 0.08 | 1 | |
| 4 <i>Potamogeton crispus</i> | 0.08 | 0.03 | 0.19 | 1 |

ton distinctus and *Potamogeton crispus*, the niche overlap between them was the next highest. This was because the two species were hygrophytic, and coexistence frequently occurred in some shallow water patches of the lower river beach.

At Stage II (table 4), the niche overlap between the dominant species *Phalaris arundinacea* and some companion species with higher niche breadth, such as *Cardamine yrata*, *Alopecurus aequalis*, *Polygonum lapathifolium*, and *Zizania caduciflora*, was higher, while in some species such as *Potamogeton crispus*, *Artemisia selengensis*, with lower niche breadth, the niche overlap between them were very low, even zero. This was because *Potamogeton crispus* and *Artemisia selengensis* are hygrophilous and terrestrial, respectively, and the environmental conditions suitable for them only occurred sporadically on the river beach at this stage.

Compared with other stages, in general, the higher niche overlap between species presented at Stage III (electronic appendix 1), particularly the niche overlap between two dominant species, was as much as 0.75. Those species with a higher niche overlap often had greater similarity in biological characteristics and/or ecological demands, which often intensified interspecific competition. Intensive interspecific competition would certainly induce the niche of some species to contract, and a resulting decrease in niche overlap among species occurred in the next succession stage.

With the succession into Stage IV, the terrestrial characteristics of environmental conditions on the river beach were displayed. The niche overlap between *Phragmites communis* and the majority of species was not very high. This was because the strong competitive ability of *Phragmites communis* rejected other species from living together or sharing common resources with it. The niche overlap between *Phragmites communis* and *Phalaris arundinacea*, however, only decreased slightly compared with the previous stage and was still as much as 0.58. This was mainly because these two species were perennial rhizome plants and not only shared large similarities in resource utilization.

The average niche overlaps of all paired species in the different succession stage communities first increased gradually and then reached the highest level at Stage III before finally decreasing slightly at Stage IV within the entire succession process (fig. 2). Statistical analysis showed there was a significant difference between any two succession stages.

Table 4 – The niche overlaps of species at Stage II along the succession process.

| Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---------------------------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|----|
| 1 <i>Phalaris arundinacea</i> | 1 | | | | | | | | | | | | | |
| 2 <i>Alopecurus aequalis</i> | 0.46 | 1 | | | | | | | | | | | | |
| 3 <i>Potamogeton distinctus</i> | 0.18 | 0.21 | 1 | | | | | | | | | | | |
| 4 <i>Potamogeton crispus</i> | 0.24 | 0. | 0.18 | 1 | | | | | | | | | | |
| 5 <i>Cardamine yrata</i> | 0.62 | 0.43 | 0.18 | 0.07 | 1 | | | | | | | | | |
| 6 <i>Limnophila sessiliflora</i> | 0.11 | 0 | 0.14 | 0.21 | 0.13 | 1 | | | | | | | | |
| 7 <i>Ranunculus sceleratus</i> | 0.33 | 0.32 | 0.16 | 0.09 | 0.21 | 0.12 | 1 | | | | | | | |
| 8 <i>Polygonum hydropiper</i> | 0.38 | 0.12 | 0.08 | 0.01 | 0.23 | 0.08 | 0.21 | 1 | | | | | | |
| 9 <i>Zizania caduciflora</i> | 0.43 | 0.13 | 0.11 | 0.11 | 0.31 | 0.12 | 0.25 | 0.18 | 1 | | | | | |
| 10 <i>Oenanthe decumbens</i> | 0.32 | 0.21 | 0.14 | 0.13 | 0.21 | 0.02 | 0.31 | 0.19 | 0.08 | 1 | | | | |
| 11 <i>Alternanthera philoxeroides</i> | 0.16 | 0.11 | 0.06 | 0.13 | 0.09 | 0.13 | 0.09 | 0.07 | 0.02 | 0.13 | 1 | | | |
| 12 <i>Hydrocharis dubia</i> | 0.21 | 0.14 | 0.11 | 0.08 | 0.13 | 0.09 | 0.06 | 0.02 | 0.04 | 0.21 | 0.1 | 1 | | |
| 13 <i>Polygonum lapathifolium</i> | 0.45 | 0.32 | 0.17 | 0 | 0.36 | 0.02 | 0.38 | 0.21 | 0.21 | 0.26 | 0.16 | 0.03 | 1 | |
| 14 <i>Artemisia selengensis</i> | 0.19 | 0.23 | 0.22 | 0 | 0.19 | 0 | 0.16 | 0.10 | 0.11 | 0.22 | 0.09 | 0.11 | 0.23 | 1 |

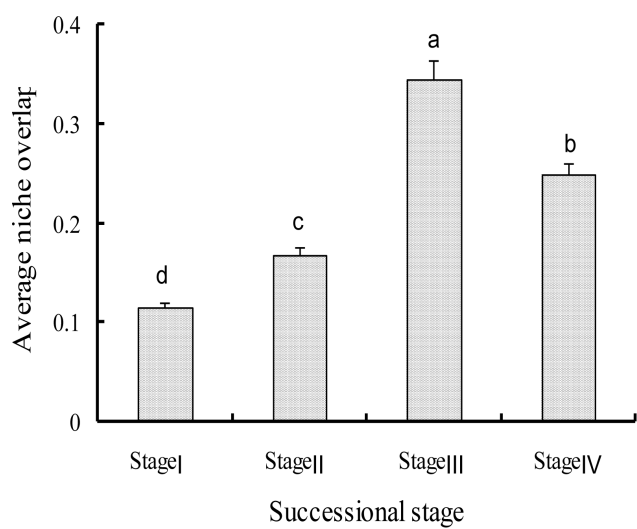


Figure 2 – The average niche overlaps of all paired species at different succession stages. The different letters on histograms indicate significant difference in average niche overlap among different successional stages at 5% level of significance.

DISCUSSION

Tables 2–4 and electronic appendices 1 & 2 demonstrate that species were rare and resources were relatively abundant at Stage I, and every species seemed to occupy a certain niche independently and expressed the state of niche segregation; the total average niche overlap of all paired species in the community was minimal (0.116). So it can be inferred that the competition in the community was much more intraspecific than interspecific, which would facilitate the expansion of species niches. New species continuously invaded, established, and occupied a certain niche and the higher niche overlap of all paired species appeared at Stage II. With the succession into Stage III, the maximum number of species occurred and the total average niche overlap of all paired species was also highest and the competition was presumably most intensive within the entire succession process. The competition in the community at this stage was much more interspecific than intraspecific. The intensive interspecies competition not only excluded some species with less adaptive faculty but also segregated and optimized niches of the remaining species, leading to a decline in total niche overlap of all paired species in the community at Stage IV. The ex-

tent of interspecific competition in the community was also weakened and most species could utilize the environmental resources more coordinately and adequately (Tokeshi & Schmid 2002). Thus, a stable equilibrium community came into being. In fact, the dynamics of average niche overlaps of all paired species in the different succession stages (fig. 2) corroborates an important ecological theory that the intraspecific competition impels species' niches to overlap, whilst the interspecific competition impels species' niches to segregate (Li et al. 2000) from the aspect of plant community succession.

As some new species invade and establish in the plant community succession process, in general, both the extent of competition and niche overlap of species will increase. Not every new species that establishes a population, however, will increase the extent of competition and niche overlap of species. The mechanisms by which new species establish populations can be classified into two broad categories. New species usurp the niches of original species through interspecific competition and this situation frequently occurs when ecologically close new and original species occur sympatrically. Alternatively, the new species can avoid intense interspecific competition with original species by utilizing minimal niche overlap (Hasegawa et al. 2010). In the present study, analysis of the niche overlap showed how some new species establish populations in the presence of some original species by minimal niche overlap with the original species or by competitive exclusion of the original species.

The ecological characteristics of a plant community, as an aggregation of plant population response to the environmental gradients, vary with the change of environmental gradients, and this change is more obvious in the succession process. These changes include those of community types, dominant species status, and the evolution of environmental conditions in habitats. The niche is a valid indicator for the relationship between species and habitats. It not only reflects the ecological adaptability and distribution range of species but also provides a description of the scarce resources for which species compete. Species with a wider niche breadth are referred to as generalist species, while species with a narrower niche breadth are considered specialist species. In general, generalist species have broad environmental tolerance and are able to use a wider range of resources that enable them to survive in more places and, hence, over a larger area than other species (Zhang et al. 2003). However, differentiation between generalist species and specialist species is often relative and not absolute. Both of them are able to convert into each other with changes in environmental conditions. The specialist species, generalist species, and conversion process of specialist-generalist species can be identified distinctly according to the niche dynamics of species in the succession process. In the case of *Cardamine yrata*, there was a conversion from generalist species at Stage II into specialist species at Stage III, while *Kalimeris indica* and *Carex cinerascens* showed a conversion from specialist species at Stage III into generalist species at Stage IV in the present study.

The dynamic characteristics of niche of species also reflect the process of displacement of species along the community succession process; here, the niche dynamics of the dominant species is especially important for plant commu-

nity succession (Zhang et al. 2003). The niche dynamics of *Phragmites communis* and *Phalaris arundinacea* exhibited the process of displacement of two species along the succession process. In the entire community succession process, *Phalaris arundinacea*-*Phragmites communis* community was only a transitional community (Fu et al. 2011). Some community characteristics, such as species most abundant, niche overlap highest, and competition most intensive often occurred at this stage. Intensive competition would inevitably make some species disappear and the niches of existing species segregate. These findings are consistent with results that show that "the higher niche overlaps reflect the instability and transition state of plant communities along the succession process" (Zhang et al. 2003). They indicated that the research results gained from wetland environments were in accordance with other research results gained from sandy land environments.

It is believed that interspecific competition is positively correlated with niche overlap, and intensive interspecific competitions often occur under the lack of common demand resources. However, some other research revealed that not all interspecific competition between species with larger niche overlap must be very intensive (Pearman et al. 2007, Kelly & Bowler 2009), because facilitation or positive interactions can sometime play a more important role than competition in stressed and resource-limited environments (Bertness & Callaway 1994). The study of facilitation is constantly maturing. There has although been the implicit assumption that facilitation mostly occurs where niche overlap is low or does not exist, otherwise competition for common resources would arise. However, this implicit assumption is being challenged in recent years. Fajardo & McIntire (2011) found that the facilitation process does occur in conspecifics under strong niche overlap. Therefore, the facilitation process is likely to also occur in interspecific interactions under strong niche overlap. In the present study, the niche overlap between *Phalaris arundinacea* and *Phragmites communis* was the higher in the entire succession process, and intensive interspecific competition between *Phalaris arundinacea* and *Phragmites communis* inevitably occurred. However, the high amount of litterfall production of these two species could provide nutrients to each other and facilitate mutual growth. This facilitation process occurred between lianas and trees, with existing intensive interspecific competition, in the tropical rainforest (Tang et al. 2012). The previous studies have shown that ecologically close species that exhibit a high degree of overlap in some niche dimensions are also able to coexist due to compensating differences in some other niche dimensions (Norberg 2000, Childress et al. 2002), while niche differences have long been identified as potential key drivers of species coexistence (Mason et al. 2011), and are able to counteract competitive effects and facilitate the coexistence of similar species (Lakkis 1994, Fargione & Tilman 2005, Takeshita et al. 2009). In fact, some significant niche differences in temporal (growth period) and spatial levels (plant height) really exist between *Phalaris arundinacea* and *Phragmites communis* (Fu et al. 2011). These niche differences, especially temporal niche difference, will certainly strengthen the two species' facilitation resulting from provision of nutrients. So it can be deduced that facilitation

process also occurs in the different species with higher niche overlap (i.e. *Phalaris arundinacea* and *Phragmites communis*).

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingen-taconnect.com/content/bothel/plecevo/supp-data>), and consist of (1) the niche overlaps of species at Stage III along the succession process; and (2) the niche overlaps of species at Stage IV along the succession process.

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