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研究課題名（英文） Mathematical analysis of species coexistence and segregating pattern formation

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研究成果の概要（和文）：外来種の侵入が拡散反応系でモデル化できる。在来種が二種、外来種が一種だとする。外来種が強ければ侵入が必ず成功して在来種が絶滅するという証明をできた。外来種が弱ければ侵入が必ず失敗することも証明できた。他の場合は、最先端解析方法を使っても現在証明をできそうにないので、二次元数値計算で三種が共することを確かめた。この場合は安定螺旋・振動する螺旋・螺旋が多い周期的なパータン・螺旋が多いカオチックなパータン等の複雑なパータンが現れている。このパータンは動いてる境界面からできていて、境界面が接触する時の相互作用の種類によってパータンの形式が変更する。境界面の相互作用が一次元の進行波を調べたら説明できる。

研究成果の学術的意義や社会的意義
We have shown how complex spatio-temporal patterns can arise from the interaction of two planarly stable fronts, without the need for instability as in other reaction-diffusion models. We have given rigorous results on the system's limit behaviour even if no vector comparison principle holds.

研究成果の概要（英文）：The ecological invasion problem in which a weaker exotic species invades an ecosystem inhabited by two strongly competing native species can be modelled by a three-species competition-diffusion system. We have proved rigorously that when the invader is very strong it will always be able to replace the native species, while it will never survive in the new environment if it is sufficiently weak. In the intermediate cases, coexistence occurs in complex spatio-temporal patterns, such as regular or breathing spirals, periodic multi-core spiral patterns or chaotic spiral turbulence. The origin of and transition between such patterns lies in the interaction of two planarly stable fronts. By studying the bifurcation structure of their one-dimensional equivalent (travelling waves), we can also understand the mechanisms governing the two dimensional case.

研究分野：　現象数理学

キーワード：　mathematical modelling　competition-diffusion　pattern formation　travelling wave　competitive exclusion　species coexistence　singular limit

１．研究開始当初の背景

As the starting point, we have to mention one of the central organizing concepts in community ecology, the law of competitive exclusion. This principle was originally proposed by a Russian ecologist, G. Gause (1934), based on his laboratory experiments on bacterial cultures. It states that two biological species competing for the same limited resources cannot coexist, resulting in the eventual extinction of one of them, that is, in competitive exclusion. As a consequence, it predicts that each species should specialize in order to find its own ecological niche (e.g., Darwin's finches on the Galápagos Islands). However, natural ecosystems often display a rich biodiversity even when resources are limited, in apparent contradiction with the principle (e.g., oceanic plankton; tropical rainforests). The understanding of the mechanisms behind such biodiversity is an active field of research in theoretical ecology. Usually species coexistence arises from the hypotheses of the principle not being satisfied, i.e., from the environment varying in space and/or time, but indirect competitive interactions may also cause coexistence. The simplest situation is to examine the possibility of coexistence of two competing native species (say, u_1 and u_2) when a third species (say, u_3) invades the ecosystem from outside. A possible model for this setting is the following three-species competition system of ODEs of Lotka-Volterra type:

where r_i, a_i, and b_{ij} are positive parameters denoting respectively the intrinsic growth rate, intra-specific and

$$(u_i)_t = u_i(r_i - a_i u_i - \sum_{j\neq i} b_{ij} u_j), \qquad (1)$$

inter-specific competition rates (i, j = 1,2,3 and i ≠ j). Equations (1) have been intensively studied from a mathematical analysis point of view (e.g., Zeeman(1993)). In particular, the possibility of coexistence of all three competing species has been intensively investigated (e.g., Gyllenberg and Yan (2009)). However, (1) is restricted to the case where movement in space of the species is negligible, so that spatially segregated coexistence cannot be discussed. For this reason, assuming the situation where each species disperses randomly in space by diffusion, a three-species competition-diffusion system can be proposed as follows:

where d_i is the diffusion rate of u_i (i = 1, 2, 3).

$$(u_i)_t = d_i \Delta u_i + u_i(r_i - a_i u_i - \sum_{j\neq i} b_{ij} u_j), \qquad (2)$$

２．研究の目的

When (2) is considered on a bounded domain with zero-flux boundary conditions, sensitively depending on the value of r_3, several different kinds of patterns are observed. In particular, for values of r_3 in a certain interval, complex spatio-temporal patterns appear and competitor-mediated coexistence occurs, despite the fact that the competitive interaction term used is the simplest nonlinear choice. Moreover, the pattern type transitions from stable regular spirals to periodic multi-spiral patterns first and then to chaotic patterns of spiral turbulence. The objective of our study was to understand the mechanism underlying such phenomena. Moreover, we aimed at proving rigorously that no coexistence was possible if r_3 was very large or very small.

３．研究の方法

Equations (2) look like simple nonlinear PDEs, but they have not been widely studied by mathematical communities, since at the moment there are no known analytical tools to successfully study such a three-component reaction-diffusion system. For this reason, we have recently developed a hybrid method combining analytic and complementary numerical tools. For example, in the study of pattern formation we have utilized numerical continuation coupled with knowledge from bifurcation theory.

４．研究成果

The complex patterns displayed by (2) are essentially composed by large regions where the species densities are constant. The interfaces between such regions move at various speeds, eventually colliding with each other. The result of this collision varies with r_3, giving rise to the different pattern typologies. Since these interfaces reduce in one spatial dimension to travelling waves, we studied in detail by numerical continuation the global bifurcation structure of such one-dimensional waves in order to shed light to the more interesting two-dimensional case. Under some assumptions on the parameters the three-species competition-diffusion system admits two planarly stable travelling waves. Their interaction in one spatial dimension may result in either reflection or merging into a single homoclinic wave, depending on the strength of the invading species. This transition can be understood by studying the bifurcation structure of the homoclinic wave. In particular, a time-periodic homoclinic wave (breathing wave) is born from a Hopf bifurcation and its unstable branch acts as a separator between the reflection and merging regimes: when a stable homoclinic wave exists, colliding waves are attracted by it resulting in merging; if the homoclinic wave is unstable, colliding waves are repulsed and reflect.

The same transition occurs in two spatial dimensions. If the waves merge in a stable homoclinic pulse then a stable regular spiral is formed, exactly as it occurs for example in the FitzHugh-Nagumo system. When r_3 is decreased, the stable regular spiral associated to the homoclinic wave destabilizes, giving rise first to an oscillating breathing spiral and then breaking up producing a dynamic pattern characterized by many spiral cores. Such pattern is initially periodic since the breakup occurs far from the spiral cores, but as r_3 is decreased it eventually leads to a chaotic pattern where the spiral cores cannot sustain themselves indefinitely and are continuously destroyed and generated anew. Finally, we remark that these complex patterns are generated by the interaction of two planarly stable travelling waves, in contrast with many other well-known cases of pattern formation where planar instability plays a central role.

Proving the appearance of coexistence rigorously appears to be quite hard at the current state of research in the field of reaction-diffusion systems. We succeeded instead in proving that coexistence is impossible, i.e., the competitive coexistence occurs, i.e., that only one species survives in the long run. This is also not trivial, because the competition-diffusion system does not admit a vector comparison principle for three or more species. However, we were able to prove our results by only employing the scalar comparison principle, applied multiple times to each single equation. In the case of a general m-species competition-diffusion system, we showed that: (1) coexistence cannot occur if one species is much stronger than the others (i.e., its growth rate r is very large), resulting in all other species becoming extinct; (2) a species will never be able to survive if its growth rate r is very low and the system will reduce to a (m-1)-species system (which for m=3 means that no coexistence can be observed). These two results are expected and, in a sense, trivial from the ecological point of view but have never been proven rigorously. Finally, we remark that we have proven the above properties both in the singular limit case (limit behavior for r tending to zero or infinity) and in the cases in which r is very large but finite or very small but positive (which are applicable to real world scenarios).

５．主な発表論文等

〔雑誌論文〕（計　2 件）

(1) L. Contento, M. Mimura

Complex pattern formation driven by the interaction of stable fronts in a competition-diffusion system Journal of Mathematical Biology, May 2019 (online publication) https://doi.org/10.1007/s00285-019-01370-3

(2) L. Contento, D. Hilhorst, M. Mimura

Ecological invasion in competition-diffusion systems when the exotic species is either very strong or very weak.

Journal of Mathematical Biology, 77(5), pp 1383–1405, Nov 2018

https://doi.org/10.1007/s00285-018-1256-4

〔学会発表〕（計　3 件）

1. ReaDiNet 2018 “Recent Progresses in Mathematical Theories for Biological Phenomena”, Jeju, Korea, Oct 2018
2. (poster) Gordon Research Seminar & Conference on Oscillations and Dynamic Instabilities in Chemical Systems, Les Diablerets, Switzerland, July 2018
3. Mathematical Biology Workshop for Ecology and Evolutionary Problems, NIMS, Daejeon, Korea., Dec 2016

〔図書〕（計　　件）

〔産業財産権〕

○出願状況（計　　件）

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権利者：
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番号：
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国内外の別：

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権利者：
種類：
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〔その他〕

ホームページ等

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