Biology of deformed Hamiltonian vector fields on Lagrangian fibrations

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Abstract

Two-component feedback loops (TCFLs) are dynamical systems arising in mathematical biology that describe the time evolution of pairs of interacting molecules using complex network theory. These dynamical systems closely resemble a Hamiltonian system in \( \mathbb{R}^{2n} \), but with the canonical equation for one of the variables in each conjugate pair rescaled by a number called the Turing instability parameter. The Turing instability parameter therefore measures the obstruction preventing a TCFL from being Hamiltonian where the Turing instability parameter equals one.

To generalise TCFLs to symplectic manifolds in this paper we introduce and study the properties of deformed Hamiltonian vector fields on Lagrangian fibrations. We describe why these objects have some interesting applications to symplectic geometry and discuss how their biological interpretation motivates new problems in Floer theory, mirror symmetry, and the study of \( \mathbb{D} \)-Kähler manifolds. Since many questions in complex network theory can be translated into the topological setting, this paper therefore serves to bring a selection of ideas from biology to pure mathematics.

Keywords: Complex networks, Symplectic geometry, Mirror symmetry, Para-Kähler manifolds, Adiabatic limits

1. Introduction

Symplectic geometry arises as the natural generalisation of Hamiltonian mechanics to differentiable manifolds. The phase space of a Hamiltonian system is generalised to a symplectic manifold and phase portraits are interpreted as integral curves of a Hamiltonian vector field. Symplectic geometry therefore has its origins in classical physics, but more recent times have
seen string theory play a role in the discovery of Gromov-Witten invariants and the birth of Floer theory. Together with mirror symmetry, these developments are some of the great success stories of symplectic geometry that can be partially attributed to mathematical physics. Very recently, dynamical systems arising in mathematical biology were also described from a symplectic viewpoint although not in the setting of differentiable manifolds [1]. The current paper grew out of an attempt to put these dynamical systems into the context of symplectic geometry and explain the biological interpretation associated with their generalisations.

Hamiltonian vector fields, which generalise dynamical systems appearing in classical mechanics, play a central role in several different versions of Floer theory for symplectic manifolds and Lagrangian submanifolds. In particular, the original motivation for Floer’s work was to find a proof for Arnold’s conjecture that the number of periodic solutions of a Hamiltonian system on a symplectic manifold is bounded below by the sum of its Betti numbers. Lagrangian Floer theory extends Hamiltonian Floer theory to pairs of Lagrangian submanifolds where Hamiltonian vector fields are used to ensure transverse intersection. This idea is further generalised by the Fukaya category, which associates to each symplectic manifold an $A_\infty$-category whose objects are its Lagrangian submanifolds. In this case Hamiltonian vector fields are required to make morphisms and higher compositions of the Fukaya category well-defined. Hamiltonian vector fields also generate a group of exact symplectomorphisms that determine the geometry of a symplectic manifold. From a different viewpoint these mathematical abstractions provide a geometric interpretation for many physical arguments, such as preservation of the phase space distribution function in Liouville’s theorem or conservation of energy along the integral curves of a Hamiltonian vector field. In light of this it is quite remarkable that Hamiltonian vector fields have such a clear physical interpretation whilst at the same time motivating (and being used as tools to solve) so many mathematical problems arising in symplectic geometry. Then again, perhaps this is not so surprising given that symplectic geometry was developed to accommodate Hamiltonian systems into a geometric setting. Can the same be achieved for the biological processes considered in [1]? This is the question that we attempt to answer here. The particular dynamical systems we shall study are closely related to Hamiltonian vector fields and a portion of this paper will be dedicated to explaining how they are related to the geometry of Lagrangian fibrations. This should not distract from the main objective however, which is to introduce these objects to the modern-day framework of symplectic geometry. Although simple in comparison
to many dynamical processes appearing in biology, at the same time our model systems are realistic enough to provide a good description of real-life biological phenomena. Thus, we shall see several examples of how biological questions can motivate new problems in mathematics.

In $\mathbb{R}^{2n}$ our dynamical systems closely resemble Hamilton’s, but with the equation for one of the variables in each conjugate pair of coordinates rescaled by a nonzero factor of $q \in \mathbb{R}$

$$
\dot{x}_i = q^{-1} \frac{\partial H}{\partial y_i}, \quad \dot{y}_i = -\frac{\partial H}{\partial x_i}.
$$

(1)

Here $H : \mathbb{R}^{2n} \to \mathbb{R}$ is a smooth function that might also depend on $q$. Equations of this form were considered a long time ago in physics and used to model dissipative phenomena \[2\]. The more recent interpretation of these systems in biological terms is described in section 2 where we also provide some mathematical background required to aid the inexperienced reader of this paper. It is clear that (1) becomes an ordinary Hamiltonian system in the limit $q \to 1$ and so to generalise these dynamical systems to symplectic manifolds we introduce the notion of a deformed Hamiltonian vector field in section 3. After proving some basic properties of deformed Hamiltonian vector fields we use them to generalise our biological systems section 4. By doing so it is revealed that many mathematical constructions have a very nice biological interpretation and consequently biological questions can be translated into the setting of symplectic geometry. One example of this is presented in section 5 where we use a Morse-type argument to propose a topological bound for the number of equilibrium solutions.

2. Preliminaries

The purpose of this section is two-fold. Firstly, to provide some biological motivation for deformed Hamiltonian vector fields and explain their physical interpretation. Secondly, to introduce the geometric objects that we will be studying throughout this paper, before fixing notation and conventions for the proceeding sections. The exposition in subsection 2.2 will be at a level suitable for those familiar with basic differential geometry and algebraic topology, and requires no previous exposure to symplectic geometry, mirror symmetry or Floer theory. Unfortunately, there is no way of including a self-contained introduction to these topics in a single paper and so in later sections we will often make the jump to assuming our reader knows a considerable amount of symplectic geometry. The hope is that by including this sort of introductory section, which may at some points seem unnecessary to the experienced reader, those unfamiliar with
modern-day concepts may be able to pick up the key ideas and be motivated to learn the relevant material before coming back to the paper at a later date.

2.1. Biological motivation

We begin by outlining the biological motivation for introducing deformed Hamiltonian vector fields. Consider a pair of biological molecules $X, Y$ whose levels or concentrations are denoted by $x, y \in \mathbb{R}$, respectively (we allow negative concentrations). A typical example is that of a protein $X$ and a ribonucleic acid $Y$, but their exact nature is not important. What is important is that we assume $X$ and $Y$ interact, either directly or indirectly, in such a way that the levels of $X$ dynamically affect the levels of $Y$ that in turn feed back to affect the levels of $X$. To model this process one studies the dynamical system

$$\begin{align*}
\dot{x} &= \frac{\partial g(y)}{\partial y}, \\
\dot{y} &= -\frac{\partial f(x)}{\partial x},
\end{align*}$$

(2)

which just says that the infinitesimal change in the levels of $X$ is determined by the infinitesimal change in some function of the total concentration of $Y$ (and vice versa, the sign is arbitrary). Functions $f$ and $g$ are called regulatory functions. The reason it is common to consider two molecules rather than three, four, etc., is that proteins and ribonucleic acids always come in pairs and so this choice is particularly natural from a biological point of view. Coincidentally, it is also a natural choice from the perspective of symplectic or complex geometry. In this case the levels of $Y$ affect the levels of $X$ directly and so $g$ is sometimes assumed to be quadratic meaning that $x$ increases linearly with $y$ [3]. Notice that these considerations imply (2) is a Hamiltonian system with Hamiltonian $H(x, y) = \frac{1}{2}y^2 + f(x)$. This is not the complete story however, since it is not only regulatory processes that can affect the levels of $X$ and $Y$. Biological molecules also have the tendency to degrade and diffuse meaning additional terms must be included on the right-hand-side of the equations (2).

When modelling spatial dependence a convenient method for describing a collection of biological cells is to imagine one cell associated with each vertex of a combinatorial graph $\mathcal{G}$ on $n$ vertices. Edges between vertices represent the possibility of a molecule moving from one cell to another and in this way $\mathcal{G}$ encodes topological information about the cellular arrangement. This procedure of diffusively coupling two-dimensional systems such as (2) was introduced by Turing in his landmark paper on pattern formation [4], and more recently by Nakao and Mikhailov [5].
Introducing diffusive coupling yields a dynamical system of the form

\[ \dot{x}_i = \frac{\partial g(y)}{\partial y_i} + q^{-1}(\Delta_G)_{ij}x_j, \quad \dot{y}_i = -\frac{\partial f(x)}{\partial x_i} - (\Delta_G)_{ij}y_j, \]

(3)

where subscripts \( i, j = 1, 2, ..., n \) denote the level of a molecule in that vertex, and \( \Delta_G = D_G - A_G \) is the discrete Laplacian defined in terms of the degree matrix, \( D_G \), and adjacency matrix, \( A_G \), of \( G \). Molecules diffuse from an area of higher concentrations to an area of lower concentrations with a speed that depends on molecular size meaning \( X \) will not necessarily move between cells at the same rate as \( Y \). This is accounted for by the parameter \( q \in \mathbb{R} \) that can be interpreted as the ratio of the diffusion coefficient of \( X \) relative to that of \( Y \). This parameter, called the Turing instability parameter, governs how solutions of (2) behave under diffusive coupling with critical values of \( q \) sometimes resulting in the formation of Turing patterns [4, 5]. It is a simple matter to check that (3) can be written in the form (1) if one takes the Hamiltonian \( H = f(x) + y \cdot \Delta_G x + qg(y) \). Thus, the Turing instability parameter \( q \) also measures the extent to which (3) has been deformed from a conventional Hamiltonian system. Biologically there are three important limits to consider. The Hamiltonian limit, \( q \to 1 \), is obtained when the diffusion coefficient of \( X \) becomes equal to minus that of \( Y \). In the Hamiltonian limit the two molecules move in opposite directions with the same speed, which is unlikely to be realized in a simple biological system. Practically speaking this means (3) will almost never be Hamiltonian unless the graph \( G \) is empty, but by taking this limit all the nice properties of Hamiltonian systems can be recovered from classical mechanics [1]. The second limit, \( q \to -1 \), is obtained when the diffusion coefficient of \( X \) becomes equal to that of \( Y \). Although once again this limit almost never occurs in practice (unless \( X \) and \( Y \) both happen to have exactly the same diffusive properties) it is a more realistic limit to take if one wants to get some approximate understanding of the dynamics governed by (3). This is complementary to the third limit, \( q \to 0 \), which describes the case where the diffusion coefficient of \( X \) becomes very large compared to that of \( Y \). In some sense the limits \( q \to 0 \) and \( q \to -1 \) can be seen as the two natural extremes of the biological system described by (3). We shall see later on that both of these limits also have a very interesting geometric interpretation.

Systems of the form (3) are called two-component feedback loops (TCFLs) [1]. They are conservative analogues of the activator-inhibitor networks first studied by Turing and many others since then (see [5] and references therein). More generally, a TCFL is a particular example
of a complex network associated with the graph $G$ where the underlying system on each vertex is just a copy of the Hamiltonian system (2). Complex networks encompass a wide range of applications from biology to physics, engineering, social sciences and economics, and in addition to pattern formation researchers working on complex networks are usually interested in collective behaviour and synchronisation. Indeed, Ren’s model for harmonic oscillator synchronisation is just a special example of a complex network obtained in the $q \to \infty$ limit of (3). Viewed as a complex network there is no reason why the coupling terms of a TCFL must be restricted to those of diffusive type. Many authors take different matrices in place of the Laplacian matrix (e.g. adjacency matrix, weighted Laplacian matrix, directed Laplacian matrix etc.) and may even include nonlinear coupling functions. It is also common for the underlying system to contain linear terms that account for *degradation* of molecules $X, Y$ with rates $\alpha, \beta \in \mathbb{R}$, respectively (see [3], Chapter 5). In this case the underlying system replacing (2) becomes

$$
\begin{align*}
\dot{x} &= \frac{\partial g(y)}{\partial y} - \alpha x, \\
\dot{y} &= -\frac{\partial f(x)}{\partial x} - \beta y,
\end{align*}
$$

which is of the form (1) with $q = -\alpha/\beta$. Taking these considerations into account the most general TCFLs we shall be interested in are

$$
\begin{align*}
\dot{x}_i &= \frac{\partial g(y)}{\partial y_i} - \alpha x_i + q^{-1} A_{ij} x_j, \\
\dot{y}_i &= -\frac{\partial f(x)}{\partial x_i} - \beta y_i - A_{ji} y_j,
\end{align*}
$$

where $A \in M(n)$ is an arbitrary square matrix. These systems can be written in the form

$$
\begin{align*}
\dot{x}_i &= q^{-1} \frac{\partial H}{\partial y_i}, \\
\dot{y}_i &= -\frac{\partial H}{\partial x_i} + \gamma y_i,
\end{align*}
$$

with Hamiltonian $H = f(x) - q\alpha y \cdot x + y \cdot Ax + qg(y)$ and constant parameter $\gamma = \beta + q\alpha$. They reduce to (1) when $q = -\beta/\alpha$, i.e. the ratio of diffusion coefficients is equal to the ratio of degradation rates, and since the underlying system (4) is no longer Hamiltonian we have a genuine example of an activator-inhibitor network. The appearance of (5) should be reminiscent of a conformal Hamiltonian system and will be assigned a geometric interpretation once deformed Hamiltonian vector fields have been defined in section 3.

From a biological perspective one may ask how many equilibrium solutions exist for a given TCFL, which determines the number of switch-like states of the biological process or co-existing stationary patterns on the network. As in the Hamiltonian case, where the Arnold
conjecture asks about the existence of periodic solutions to Hamilton's equations, a related concept is to provide a lower bound on the number of periodic solutions. A version of this problem was proposed by Smale [11] for activator-inhibitor networks where the underlying system is dissipative, but for TCFLs where the underlying system is Hamiltonian the natural analogue involves periodic orbits of time-varying complex networks [12]. The biological interpretation of (5) with diffusive coupling evolving over time is one that describes the dynamics of a TCFL on a growing cellular network. Given the close relationship between TCFLs and Hamiltonian systems one might hope that tools used to study the former may be adapted from the latter. The work in [1] went some way towards addressing this problem. In this paper we shall be concerned with an alternative approach, which is to see how far one can get by generalising TCFLs to spaces with nontrivial topology in the same way that Hamiltonian systems are generalised by Hamiltonian vector fields. Spaces of more interesting topology could arise biologically in a number of ways, the most obvious example being when some external constraints or relations are imposed on \((x, y)\)-phase space. Introducing generalised TCFLs as deformed Hamiltonian vector fields also raises specific questions in symplectic geometry and the existence of periodic solutions may be addressed using a modified version of Floer theory. In the next subsection we summarise some of the mathematical background that is required for the remainder of this paper.

2.2. Geometric background

By \((M, \omega)\) we will denote a differentiable manifold \(M\) of dimension \(2n\) equipped with a closed and non-degenerate 2-form \(\omega\) called the symplectic form. Symplectic manifolds always admit an almost complex structure, i.e. an automorphism \(J : TM \rightarrow TM\) of the tangent bundle satisfying \(J^2 = -id\), and \(J\) is said to be compatible with \(\omega\) if \(G(\cdot, \cdot) = \omega(\cdot, J\cdot)\) is a Riemannian metric on \(M\). We call \(G\) the standard Riemannian metric associated with \(J\). If the Nijenhuis tensor associated with \(J\) vanishes then \(J\) is said to be integrable and \((M, J)\) complex. If \(J\) is both integrable and compatible with \(\omega\) then the triple \((M, \omega, J)\) is called Kähler and the induced metric \(G\) is called a Kähler metric. Equivalently, one may instead take as a starting point the pair \((M, G)\) where \(M\) is a complex \(n\)-fold, defined as having an atlas of charts to the open disk in \(\mathbb{C}^n\), and \(G\) the real part of a hermitian form (the complex analogue of a Riemannian metric on \(M\)). If the imaginary part of the hermitian form is a symplectic form on \(M\) then \((M, G)\) is again said to be Kähler. Both viewpoints are equivalent in the sense that one can think of the triple \((\omega, J, G)\) on an equal
footing or, as is more common when it comes to mirror symmetry, taking a Kähler metric as the starting point and varying the complex or symplectic structures independently. Hence, there are two natural types of local coordinates on a Kähler manifold: complex (holomorphic), where $M$ is typically considered as a complex $n$-fold, and symplectic (Darboux) coordinates where $M$ is considered as a real $2n$-dimensional manifold. Throughout most of this paper we will concern ourselves with the symplectic viewpoint and not worry whether or not $M$ is Kähler; in section 4 we will need to understand both viewpoints however, since mirror symmetry is conjectured to interchange the two.

Recall that a submanifold $L \subset M$ of a symplectic manifold $(M, \omega)$ is called *Lagrangian* if $L$ is half the dimension of $M$ and $\omega$ vanishes when restricted to $L$. A theorem of Weinstein says that a sufficiently small neighbourhood of a Lagrangian submanifold $L \subset M$ can always be identified with a neighbourhood of the zero section in $T^*L$ by a diffeomorphism that preserves the symplectic form (i.e., a symplectomorphism). By a Lagrangian fibration $\pi : (M, \omega) \to B$ we mean a smooth fibration $\pi : M \to B$ over an $n$-dimensional base manifold $B$ such that at every point $x \in B$ the fibre $F_x = \pi^{-1}(x)$ is a Lagrangian submanifold of the symplectic manifold $(M, \omega)$. The obvious noncompact examples are cotangent bundles $\pi : T^*B \to B$ where the zero section is canonically identified with $B$, but it is rare to find particularly exotic examples of compact Lagrangian fibrations without singular fibres. The Arnold-Liouville theorem says that locally a Lagrangian fibration with compact, connected fibre is affinely isomorphic to the product of an affine space with a torus. Indeed, each compact, connected fibre of a smooth Lagrangian fibration must necessarily be a torus and the base must have canonical *integral affine structure*. This means that $B$ admits an atlas of coordinate charts whose transition functions are elements of the affine group $\mathbb{R}^n \rtimes GL(n, \mathbb{Z})$.

After choosing a compatible almost complex structure $J$ on the total space of a Lagrangian fibration $\pi : (M, \omega) \to B$ the standard Riemannian metric $G$ induces a decomposition of the tangent bundle $TM$ into vertical and horizontal subspaces

$$TM = TB \oplus TF \, M \, .$$

The subspace $TF \, M$ is the tangent space to the fibres of $\pi : (M, \omega) \to B$ and $TB \, M$ is its $G$-orthogonal complement. This in turn corresponds to a decomposition of the metric

$$G = GB \oplus GF \, ,$$

8
where $G_B$ can often be identified with the pull-back under the projection of some Riemannian metric on $B$ (that we also call $G_B$ when it is understood). $G_F$ is the part that annihilates the orthogonal complement of the fibres. As above we prefer to speak of the choice of almost complex structure determining $G$, but it will sometimes be convenient to view the almost complex structure as being determined by a choice of metric on $B$. One such example is the analogue of the Sasaki metric $G_{\text{Sas}}$ [13] for the cotangent bundle $T^*B$ of a Riemannian manifold $(B, G_B)$ that uniquely determines an almost complex structure $J_{\text{Sas}} : G_{\text{Sas}}(\cdot, \cdot) = \omega(\cdot, J_{\text{Sas}} \cdot)$. Here $\omega = d\theta$ is the canonical symplectic form where $\theta$ is the tautological 1-form on the cotangent bundle $T^*B$. The pair $(T^*B, \omega)$ is naturally a symplectic manifold and the fibres of $\pi : (T^*B, \omega) \to B$ are Lagrangian submanifolds.

Alongside the decomposition of $TM$ induced by the choice of $J$ there is a corresponding decomposition of the cotangent bundle

$$T^*M = (T^B M)^* \oplus (T^F M)^*, \quad (9)$$

where $(T^B M)^*$ is the annihilator of $T^F M$ and $(T^F M)^*$ is that of $T^B M$. This induces a bigrading on differential forms of degree $a$

$$\Omega^a(M) = \bigoplus_{b+c=a} \Omega^{b,c}(M), \quad (10)$$

with $\Omega^{b,c}(M)$ denoting the space of sections of $\wedge^b(T^B M)^* \otimes \wedge^c(T^F M)^*$. Whenever there is such a splitting of differential forms the de Rham differential $d$ can be written as a sum of four components

$$d = d_{1,0} + d_{0,1} + d_{2,-1} + d_{-1,2}, \quad (11)$$

where $d_{c,d} : \Omega^{a,b}(M) \to \Omega^{a+c,b+d}(M)$. We say that $\alpha \in \Omega^a(M)$ is of type $(b,c)$ if $\alpha \in \Omega^{b,c}(M)$. The Lagrangian condition together with non-degeneracy of the symplectic form implies $\omega$ is of type $(1,1)$. Whilst commonplace in Kähler geometry, such decompositions of forms and exterior derivatives rarely have applications outside the world of complex manifolds because a priori they depend on the choice of almost complex structure and do not encode the same sort of topological information as the Dolbeault decomposition. However, this decomposition will provide us with an intuitive viewpoint for the construction presented in the following section. For integrability reasons the operator $d_{-1,2}$ vanishes when $\pi : M \to B$ is a smooth fibration so that after dropping
the annoying indices by defining

\[ \delta := d_{2,-1}, \quad \partial_+ := d_{1,0} \quad \text{and} \quad \partial_- := d_{0,1} \]  \hspace{1cm} (12)

the exterior derivative reduces to

\[ d = \partial_+ + \partial_- + \delta . \]  \hspace{1cm} (13)

Using \( d^2 = 0 \) one obtains the relations

\[ \partial_-^2 = \delta^2 = \partial_+ \partial_- + \partial_- \partial_+ = \partial_+ \delta + \delta \partial_+ = \partial_+^2 + \partial_- \delta + \delta \partial_- = 0 . \]  \hspace{1cm} (14)

The identity \( \partial_-^2 = 0 \) is attributed to the fact we have an involutive distribution on \( M \) induced by the vertical directions of the fibration. Obstruction to the identity \( \delta = 0 \) comes down to the fact that the \((G\text{-orthogonal})\) complementary distribution might not necessarily be integrable. If it were, \( M \) would admit a pair of transversal Lagrangian foliations that, although entirely possible, is a rather strict condition to impose. Manifolds with this property have been called bi-Lagrangian, para-Kähler or \( \mathbb{D}\text{-Kähler} \) in the literature \[14, 15, 16, 17\]. In this paper however, we shall reserve the phrase bi-Lagrangian for integrability of the \( J \)-induced complementary distribution of an existing Lagrangian fibration, i.e. \((M, \omega, J)\) is bi-Lagrangian if and only if \( \delta = 0 \).

Given a smooth function \( H : M \to \mathbb{R} \) the Hamiltonian vector field \( X_H \in TM \) on \((M, \omega)\) is the unique vector field defined by

\[ \omega(X_H, \cdot) = -dH . \]  \hspace{1cm} (15)

By Liouville’s theorem \( X_H \) generates an (exact) symplectomorphism of \( M \) because its flow preserves the symplectic form

\[ L_{X_H}(\omega) = d(\omega(X_H, \cdot)) = -d^2H = 0 , \]  \hspace{1cm} (16)

where \( L_{\xi} \) denotes the Lie derivative along the flow of the vector field \( \xi \). \( X_H \) uniquely defines a gradient vector field because of the fact that

\[ G(JX_H, \cdot) = \omega(X_H, \cdot) = -dH , \]  \hspace{1cm} (17)

and so one may identify \( JX_H \) with \(-\nabla H\), the gradient of \(-H\) taken with respect to the standard Riemannian metric associated with \( J \). If \( H(t) = H(t + 1) : M \to \mathbb{R} \) defines a 1-periodic family
of functions parameterised by $t \in S^1$ then it generates a family of exact symplectomorphisms $\phi_t : M \to M$ via
\[
\frac{d}{dt} \phi_t = X_{H(t)} \circ \phi_t , \quad \phi_0 = id .
\] (18)
The Arnold conjecture states that for $M$ closed the number of non-degenerate 1-periodic solutions of the associated differential equation
\[
\dot{z}(t) = X_{H(t)}(z(t)) ,
\] (19)
is bounded below by the sum of the Betti numbers of $M$.

We now briefly outline the basics of Floer theory that lead to a proof of the Arnold conjecture for Hamiltonian flows [18]. For a given symplectic manifold $(M, \omega)$ let $LM$ be the space of contractible loops in $M$ and $\{J_t\}$ a 1-periodic family of almost complex structures compatible with $\omega$ for each value of $t \in S^1$. Define
\[
\mathcal{P}(H) = \{z \in LM \mid (19)\} .
\] (20)
The Arnold conjecture says that if the elements of $\mathcal{P}(H)$ are nondegenerate in the sense that
\[
\det(1 - d\phi_1(z(0))) \neq 0 ,
\] (21)
then for $M$ closed one has
\[
\#\mathcal{P}(H) \geq \sum_{a=0}^{2n} \dim H_a(M) ,
\] (22)
where $H_a(M)$ denotes the $a$th singular homology group of $M$. To prove (22) Floer considered smooth maps $u : \mathbb{R} \times S^1 \to M$ that satisfy the partial differential equation
\[
\frac{\partial u}{\partial s} + J_t(u) \left( \frac{\partial u}{\partial t} - X_{H(t)}(u) \right) = 0 ,
\] (23)
with boundary conditions $u(s, 0) = u(s, 1)$ and
\[
\lim_{s \to \pm \infty} u(s, \cdot) = z^\pm \in \mathcal{P}(H) .
\] (24)
In a certain sense this equation can be seen as the negative gradient flow of an action functional of the universal cover of $LM$ and so extending Morse theory to an infinite-dimensional setting Floer constructed an invariant of $M$ (now called Floer homology) involving counts of these solutions. The Floer chain complex, $CF_\ast(H, J)$, has as its generators the periodic orbits $\mathcal{P}(H)$ and the differential counts perturbed pseudo-holomorphic curves (i.e. solutions to
the Floer equation) between them. Under suitable conditions the associated Floer homology, $HF_*(H, J)$, is independent of the choices made for $H$ and $J$. Thus, in the special case where $H$ is chosen to be $t$-independent the Floer equation reduces to a gradient flow equation on $M$ and therefore $HF_*(H, J)$ agrees with the singular homology $H_*(M)$. Since the number of periodic solutions generating $CF_*(H, J)$ is bounded below by the dimension of $HF_*(H, J)$ this proves the Arnold conjecture for closed manifolds. Floer also introduced a related version of his chain complex that has as its generators the intersection points of two transversely intersecting Lagrangian submanifolds $L_0, L_1 \subset M$ \cite{19}. Introducing an infinite-dimensional analogue of Morse theory along the same lines as Hamiltonian Floer theory led him to consider solutions of the Cauchy-Riemann equation for pseudo-holomorphic curves $u : \mathbb{R} \times [0, 1] \to M$ that satisfy boundary conditions $u(s, 0) \in L_0, u(s, 1) \in L_1$. Floer proved that the Lagrangian version of his theory again gives rise to a well-defined chain complex, $CF_*(L_0, L_1)$, provided appropriate conditions are imposed on the Lagrangians and ambient symplectic manifold (e.g. $\pi_2(M, L) = 0$ to avoid contributions from pseudo-holomorphic discs). In particular, he demonstrated that the associated homology, $HF_*(L_0, L_1)$, remains invariant under the action of a Hamiltonian symplectomorphism $\phi_H$ in the sense that $HF_*(L_0, L_1) \cong HF_*(L_0, \phi_H(L_1))$. He also proved that $HF_*(L, L) \equiv HF_*(L, \phi_H(L)) \cong H_*(L)$ when $\phi_H$ is chosen to ensure transverse intersection.

3. Deformed Hamiltonian vector fields

We are now in a position to define the objects of primary interest to this paper. As described in subsection 2.1, the initial motivation for introducing deformed Hamiltonian vector fields is to provide a geometric framework for the dynamical systems $\mathbf{1}$. A particular choice of Hamiltonian means that $q \in \mathbb{R}$ can be interpreted as the Turing instability parameter and in this case systems the form $\mathbf{1}$ arising naturally in the biological sciences describe TCFLs on a graph $G$ \cite{1}. Dynamical systems resembling $\mathbf{1}$ also appear in physics \cite{2} and so deformed Hamiltonian vector fields can be viewed as a generalisation of those ideas as well. After defining deformed Hamiltonian vector fields we will prove several properties that explain how they are related to their ordinary Hamiltonian counterparts. We will also discuss some of the issues surrounding a deformed analogue of Floer theory and why a deformed Arnold conjecture seems far from reach at present.

As before, let $\pi : (M, \omega) \to B$ be a Lagrangian fibration of a symplectic manifold $(M, \omega)$ and
pick a smooth function $H : M \to \mathbb{R}$. Choose an almost complex structure $J$ on $M$ compatible with $\omega$ and consider the natural decomposition of the tangent bundle and standard metric

$$T^*M = T^B M \oplus T^F M, \quad G = G_B \oplus G_F. \tag{25}$$

The one-parameter family of metrics $\{G_q\}$ is formed by rescaling the metric in the fibre direction so that for each fixed value of $q \in (0, 1]$ we have a Riemannian metric

$$G_q = G_B \oplus qG_F \tag{26}$$

(we postpone the discussion of what happens for negative $q$ until the next section). Then $\{(M, G_q)\}$ defines a family of Riemannian manifolds with fibres whose volumes are monotonically decreasing as $q \to 0$. However, as before we prefer to view $\{G_q\}$ as being determined by the almost complex structures $\{J_q\}$ and consider the family $\{(M, \omega, J_q)\}$ defined by requiring that $G_q(\cdot, \cdot) = \omega(\cdot, J_q \cdot)$ for each $q \in (0, 1]$. Using the decomposition of the exterior derivative induced by the Lagrangian fibration we also introduce a family of operators $\{d_q\}$ to go alongside this family of degenerating symplectic manifolds.

**Definition 1.** For fixed $q \in (0, 1]$ the deformed exterior derivative $d_q$ is given by

$$d_q := \partial_+ + q^{-1}\partial_- + q\delta. \tag{27}$$

The following proposition confirms that for each $q \in (0, 1]$ the operator $d_q$ is a well-defined differential on $\Omega^*(M)$.

**Proposition 1.** $d_q^2 = 0$.

**Proof.** We have $d_q^2 = \partial_+^2 + \partial_-\delta + \delta\partial_- + q(\partial_+\delta + \delta\partial_+) + q^{-1}(\partial_-\partial_+ + \partial_+\partial_-) + q^2\delta^2 + q^{-2}\partial_-^2$ and by (14) every term multiplying a given power of $q$ vanishes. \hfill \Box

It must be emphasised that the definition of $d_q$ is only possible because we have a decomposition of the exterior derivative (13) that depends on the Lagrangian fibration and also the choice of almost complex structure $J$. Therefore the two families $\{d_q\}$ and $\{J_q\}$ are not independent and when we refer to one element, $d_q$, say, we will always have a corresponding object, $J_q$, in the other family. It is important to bear this in mind since this leads to two equivalent definitions of a deformed Hamiltonian vector field.
**Definition 2.** The deformed Hamiltonian vector field generated by $H$ is the unique vector field $X^q_H \in TM$ that satisfies

$$\omega(X^q_H, \cdot) = -d_q H.$$  \hspace{1cm} (28)

This generalises the usual definition of a Hamiltonian vector field since $q$ serves as a “deformation parameter” for the exterior derivative in the sense that we return to the classical definition in the limit $q \rightarrow 1$. Once more we have actually defined an entire family $\{X^q_H\}$ parameterised by $q \in (0, 1]$ and by writing $X^q_H$ we are referring to the deformed Hamiltonian vector field corresponding to $d_q$ and $J_q$. The next proposition provides an equivalent definition for $X^q_H$ in terms of the metric $G_q$.

**Proposition 2.** Given a deformed Hamiltonian vector field $X^q_H$, the vector field $JX^q_H$ is the gradient of $-H$ defined using the metric $G_q$.

**Proof.** We want to show that $G_q(JX^q_H, Y) = -dH(Y)$ for all $Y \in TM$. Using the decomposition of $TM$ we write the vector field $Y \in TM$ as $Y = Y_+ + Y_-$ where $Y_+ \in TB M$ and $Y_- \in TF M$. Note $\delta = 0$ when acting on functions so that

$$-d_q H(Y) = -\partial_+ H(Y_+) - q^{-1} \partial_- H(Y_-)$$  \hspace{1cm} (29)

and using $\omega$-compatibility of $J$ we have

$$\omega(X^q_H, Y) = G_B(JX^q_H, Y_+) + G_F(JX^q_H, Y_-).$$  \hspace{1cm} (30)

We define the new vector field $Y^q$ by setting $Y^q_+ = Y_+$ and $Y^q_- = q^{-1} Y_-$ and after equating both of the expressions above obtain

$$-dH(Y^q) = G_B(JX^q_H, Y^q_+) + qG_F(JX^q_H, Y^q_-) = G_q(JX^q_H, Y^q),$$  \hspace{1cm} (31)

which proves the proposition. \hfill $\Box$

Thus, the vector field $JX^q_H$ on the manifold $(M, \omega, J)$ is defined to be the vector field that would be a gradient with respect to the standard Riemannian metric on the manifold $(M, \omega, J_q)$. That is to say, $JX^q_H = -\nabla_q H$ where $\nabla_q$ is the gradient associated with $G_q$. Although somewhat more convoluted, this definition makes explicit the choice of almost complex structure in the construction of a deformed Hamiltonian vector field.
The first definition of a deformed Hamiltonian vector field is more natural from the perspective of understanding the flow of $X^q_H$ and also because geometric properties of the Lagrangian fibration $\pi : (M, \omega) \to B$ are reflected in the analytic properties of $d_q$. It turns out that these properties are tied up with the particular choice of function $H$ used to generate the deformed Hamiltonian vector field. We will now describe what this means.

**Definition 3.** Functions $H : M \to \mathbb{R}$ satisfying the property $\partial_- \partial_+ H = 0$ are called simple, whilst functions satisfying $\partial_+ H = 0$ are called exceptionally simple.

It is obvious that exceptionally simple implies simple, but the converse is not true. The exceptionally simple condition is intrinsic to the fibration whereas the simple condition depends on the choice of almost complex structure. Sometimes it will prove useful to decompose the function $H$ as $H = H_+ + \hat{H} + H_-$ where $\partial_\pm H_\mp = 0$. $\hat{H}$ is the part of $H$ that is not necessarily simple nor exceptionally simple, and in particular one has that $\partial_+ \partial_- H = \partial_+ \partial_- \hat{H}$ since $H_+ + H_-$ is simple. Of course this decomposition is not unique, but we assume it is “maximal” in the sense that $\hat{H} = 0$ whenever possible. To get a feel for what the simple condition really means we choose a Darboux coordinate chart $\{x_i, y_j\}$ for $T^*\mathbb{R}^n$ as a model for the Lagrangian fibration $(M, \omega, J)$ in which $\{x_i\}$ are coordinates on the base $\mathbb{R}^n$ and $\{y_i\}$ are coordinates on the fibres. A generic Hamiltonian is just an arbitrary function $H(x, y)$ of all the coordinates and one finds that

$$\partial_- \partial_+ H(x, y) = \frac{\partial^2 H}{\partial y_i \partial x_j} dy_i \wedge dx_j , \quad (32)$$

so that $H$ being simple is equivalent to $H(x, y) = H'(x) + H''(y)$. Likewise, $H$ being exceptionally simple is equivalent to setting $H(x, y) = H''(y)$ as a function of the fibre coordinates only. The following proposition describes how the flow of $X^q_H$ depends on the choice of Hamiltonian $H$ by answering the question of when a deformed Hamiltonian field generates a symplectomorphism.

**Proposition 3.** For $q \neq 1$ a deformed Hamiltonian vector field $X^q_H$ on $(M, \omega, J)$ is symplectic if $H$ is of the form $H = H_+ + H_-$ with $\partial_\pm H_\mp = 0$. If, in addition, $(M, \omega, J)$ is bi-Lagrangian then the flow of $X^q_H$ is symplectic if and only if $H$ is simple.

**Proof.** After a straightforward calculation it becomes clear that in general $X^q_H$ does not generate a symplectomorphism unless $q = 1$ since the 1-form $d_q H$ is not necessarily closed

$$L_{X^q_H}(\omega) = -dd_q H = (q^{-1} - 1)(\partial_+^2 + \partial_- \partial_+) H . \quad (33)$$
The 2-forms $\partial^2_+ H$ and $\partial_- \partial_+ H$ are of different type and so we cannot have $- \partial^2_+ H = \partial_- \partial_+ H$ unless both are zero, hence proving that $H$ must be simple if $\partial^2_+ = 0$. Using relations (14), if $H = H_+ + H_-$ then $\partial^2_+ H = \partial^2_+ H_+ = - \delta \partial_- H_+ = 0$ and so this condition is sufficient whenever $(M, \omega, J)$ is not bi-Lagrangian.

We may also ask when a deformed Hamiltonian vector field is conformally symplectic, i.e. generates a conformally symplectic diffeomorphism $\phi : M \to M$ that preserves the symplectic form up to some constant $1 \neq c \in \mathbb{R}$. The conformal symplectomorphisms form a group that, like the group of symplectomorphisms, is one of Cartan’s six classes of groups of diffeomorphisms on a manifold $M$. Conformally symplectic vector fields have previously been used to generalise simple mechanical systems with dissipation [9]. The proposition below answers the question of when a deformed Hamiltonian vector field is conformally symplectic on a bi-Lagragian manifold.

**Proposition 4.** For $q \neq 1$ a deformed Hamiltonian vector field $X^q_H$ on bi-Lagragian $(M, \omega, J)$ is conformally symplectic if and only if $\omega = c' \partial_- \partial_+ H$ for some nonzero constant $c' \in \mathbb{R}$.

**Proof.** When $(M, \omega, J)$ is bi-Lagrangian the condition that $X^q_H$ generates a conformal symplectomorphism is that

$$L_{X^q_H}(\omega) = -dd_q H = (q^{-1} - 1) \partial_- \partial_+ H = c \omega$$

for some nonzero constant $c \in \mathbb{R}$. Clearly this implies $\omega = c^{-1}(q^{-1} - 1) \partial_- \partial_+ H$. □

Thus, on a bi-Lagrangian manifold $(M, \omega, J)$ a deformed Hamiltonian vector field $X^q_H$ is conformally symplectic whenever $\omega = \partial_- \partial_+ K$ is defined globally by the analogue of a Kähler potential $K : M \to \mathbb{R}$ with $H = H_+ + K + H_-$ satisfying $\partial_\pm H_\mp = 0$. This is yet again a very strict condition to impose on a symplectic manifold since, as in the Kähler case, when $(M, \omega, J)$ is bi-Lagrangian $\omega$ is usually only determined by a potential locally [17]. Examples of these manifolds do exist however. Note that because $\omega$ is necessarily of type $(1, 1)$ Proposition 4 breaks down when $(M, \omega, J)$ is not bi-Lagrangian unless we impose the additional condition that $\partial^2_+ H$ vanishes. We can not ask for $H$ to be exceptionally simple (our definition of a conformally symplectic vector field excludes the symplectic case), so $H$ must be a non-simple Hamiltonian that satisfies $\partial^2_+ H = 0$ with $\omega = c' \partial_- \partial_+ H$. This further restricts the types of functions that may be considered. Different types of deformed Hamiltonian vector fields are defined by allowing the
Hamiltonian to also depend on the deformation parameter and weighting various components in a decomposition of $H$ by factors of $q$. In this case the Hamiltonian associated with $d_q$ and $J_q$ will be denoted by $H_q$. For example, given a decomposition $H = H_+ + \hat{H} + H_-$ we may form the new Hamiltonian $H_q = H_+ + \hat{H} + qH_-$ and consider the associated family $\{H_q\}$. There are an infinite number of ways of constructing these families from any one Hamiltonian, and although differences between them appear subtle they play an essential role when taking limits of objects depending on $q$. However, we will only really be concerned with the family provided in the example above since the motivating biological system is described by a Hamiltonian of this form. A detailed analysis of the relationships between deformed Hamiltonian vector fields generated by different $H_q$ would be the subject of another paper since it invariably depends on the particular application to symplectic geometry that one might have in mind. It suffices to say that any algebra generated by these objects would certainly be very different from that of Hamiltonian vector fields since there is no straightforward way of closing a collection of deformed Hamiltonian vector fields under the action of the Lie bracket. Whether or not certain subsets of deformed Hamiltonian vector fields generate deformed versions of a Lie algebra remains an open question.

As in the Hamiltonian case, a deformed Hamiltonian vector field $X_H^q \in TM$ determines a differential equation

$$\dot{z}(t) = X_H^q(z(t)),$$

which is the appropriate generalisation of (1). With a time-dependent Hamiltonian $H : S^1 \times M \to \mathbb{R}$ there is an associated two-parameter family of diffeomorphisms $\phi_t^q : M \to M$ generated via

$$\frac{d}{dt} \phi_t^q = X_{H(t)}^q \circ \phi_t^q, \quad \phi_0^q = id,$$

for each value of $q \in (0,1]$. These are symplectomorphisms when $H(t) = H_+(t) + H_-(t)$ (or conformal symplectomorphisms when $H(t)$ and $(M, \omega, J)$ satisfy the requirements of Proposition 4), but in general they do not preserve $\omega$ unless $q = 1$. As already explained in subsection 2.1, once generalised TCFLs have been defined as a particular type of deformed Hamiltonian vector field the number of periodic solutions to a time-dependent version of (35) is an important biological question. In light of the previous discussion however, it would not be prudent to formulate a deformed analogue of the Arnold conjecture for solutions to a time-dependent version of (35), even with the assumption that $|1-q|$ is sufficiently small. The diffeomorphisms generated
by deformed Hamiltonian vector fields fail to form a group in the same way that Hamiltonian symplectomorphisms do and it can not be ruled out that nice properties such as the existence of fixed points on closed manifolds are destroyed as soon as \( q \) moves infinitesimally away from \( 1 \). That being said, we can think of no explicit examples where this turns out to be the case. Moreover, when \( H \) is independent of time the Arnold conjecture follows trivially from the fact that the critical points of \( H \) are constant solutions of (35) and therefore 1-periodic. Non-degeneracy of the solutions implies \( H \) is a Morse function and the result follows from elementary Morse theory and its independence from the choice of metric on \( M \). It therefore seems plausible to see how far one can get following the approach of Floer and studying solutions of the partial differential equation

\[
\frac{\partial u}{\partial s} + J_t(u) \left( \frac{\partial u}{\partial t} - X^q_{H(t)}(u) \right) = 0 ,
\]

for smooth maps \( u : \Sigma \to M \) from a Riemann surface \( \Sigma \) with appropriate boundary conditions. Two remarks are in order before outlining the analytic complications that arise when working with this deformed Floer equation.

1) Solutions that do not depend on \( s \) satisfy

\[
\frac{du}{dt} = X^q_{H(t)}(u) ,
\]

so are solutions of the time-dependent version of the differential equation (35). Naively one expects solutions of the deformed Floer equation to converge to orbits of \( X^q_{H(t)} \) in the limit \( |s| \to \infty \). This would mean that solutions could be interpreted as flow lines connecting these orbits as points in some infinite-dimensional space. The problem is that in order to prove convergence one requires a bound on the energy of a solution. In Floer theory this bound is obtained from a perturbed symplectic action functional, but this does not appear to exist for deformed Hamiltonian vector fields.

2) If \( H \) does not depend on time then time-independent solutions to the deformed Floer equation (37) satisfy

\[
\frac{du}{ds} + \nabla q H(u) = 0 .
\]

These trajectories are flows of the gradient of \( -H \) defined with respect to the deformed metric \( G_q \). In the usual approach to the Arnold conjecture one first proves that Floer homology remains
invariant under the choice of a time-independent Hamiltonian and that Floer trajectories are in bijection with gradient flow lines of \(-H\). Thus, one proves that Morse and Floer differentials coincide. At first glance it looks as if a similar argument should apply to the deformed Floer equation \(37\) provided one could prove a homology defined by counts of its solutions remains invariant under a choice of time-independent Hamiltonian.

Besides the fact that there is no analogue of a perturbed symplectic action functional, readers who are familiar with Floer theory at the level of Salamon’s lecture notes [20] will realise that proving transversality and compactness (which again relies on existence of an energy bound) for the deformed Floer equation is not straightforward at all. The operator obtained after linearising (37) in a trivialising chart is of the form

\[ D_q = \frac{d}{ds} - A_q(s), \tag{40} \]

where \(A_q(s) : W^{1,p} \to L^p\) are a family of operators between appropriate Sobolev spaces that are not self-adjoint unless \(q = 1\). Hence, the requisite analysis used to prove \(D_q\) is Fredholm with index expressed in terms of the Conley-Zehnder indices [21, 22] will not go through and one needs to understand the Fredholm property and spectral flow problem from the perspective of hyperbolic operators [23]. We will not elaborate upon this fact except to say that there is an additional complication that in general the spectral flow of \(A_q(s)\), and hence the dimension of the corresponding moduli spaces, might also have irregularities at certain values on \(q\). It therefore seems that a Floer-type theory for deformed Hamiltonian vector fields is well beyond the scope of methods available to the field at present. In section 5 we resort to considering a model for deformed Floer theory that is designed to expand upon point 2 above. Namely, we consider a finite-dimensional gradient flow problem on a Lagrangian fibration equipped with the metric \(G_q\). In the next section we shall use deformed Hamiltonian vector fields to define generalised TCFLs on exact Lagrangian fibrations and describe the biological interpretation of their geometric properties. It should be pointed out that deformed Hamiltonian vector fields already provide a geometric interpretation of the physical systems considered in [2].
4. Generalised TCFLs

In this section we return to the original motivation for introducing deformed Hamiltonian vector fields and use them to define TCFLs on exact symplectic manifolds equipped with the structure of a Lagrangian fibration. That generalised TCFLs are naturally suited to cases where the underlying symplectic manifold is exact should come as no surprise given the observation in subsection 2.1 that TCFLs closely resemble conformal Hamiltonian systems. The aim of this section is to assign some geometric meaning to the characterising biological features of a generalised TCFL, namely the Turing instability parameter and complex network structure. In turn, the biological viewpoint raises several questions that do not seem to have been considered in symplectic geometry previously. These new ideas include the appearance of $\mathbb{D}$-Kähler manifolds in mirror symmetry and the concept of synchronisation in dynamical systems defined on arbitrary differentiable manifolds.

4.1. Exact Lagrangian fibrations and Lagrangian torus fibrations

Throughout this section we shall assume that $(M, \omega)$ is an exact symplectic manifold with symplectic form $\omega = d\theta$ meaning that $M$ in necessarily noncompact. On an exact symplectic manifold one obtains a conformally symplectic vector field $X_\gamma \in T M$ by setting $\omega(X_\gamma, \cdot) = \gamma \theta$ for some constant $\gamma \in \mathbb{R}$. The conformal Hamiltonian vector field $X_{\gamma, H}$ generated by the Hamiltonian $H : M \to \mathbb{R}$ is defined by

$$\omega(X_{\gamma, H}, \cdot) = -dH + \gamma \theta,$$

which satisfies $L_{X_{\gamma, H}}(\omega) = \gamma \omega$. This implies that the flow of $X_{\gamma, H}$ is conformally symplectic in the sense of [9]. If $\pi : (M, \omega) \to B$ is also a Lagrangian fibration equipped with a choice of $\omega$-compatible almost complex structure we can take this construction one step further using the deformed exterior derivative $d_q$.

**Definition 4.** The deformed conformal Hamiltonian vector field generated by $\gamma$ and $H$ is the unique vector field $X_{\gamma, H}^q \in TM$ that satisfies

$$\omega(X_{\gamma, H}^q, \cdot) = -d_q H + \gamma \theta.$$  

The above definition simply states that a deformed conformal Hamiltonian vector field $X_{\gamma, H}^q$ is the sum of the deformed Hamiltonian vector field $X_{\gamma, H}^q$ and conformally symplectic vector...
field $X_γ$. Generalised TCFLs will now be defined in terms of these using a particular choice of Hamiltonian. Recall from subsection 2.1 that the TCFL
\[
\dot{x}_i = \frac{\partial g(y)}{\partial y_i} - \alpha x_i + q^{-1} A_{ij} x_j, \quad \dot{y}_i = -\frac{\partial f(x)}{\partial x_i} - \beta y_i - A_{ji} y_j,
\]
(43)
describes the time-evolution of levels of interacting molecules $X, Y$ with functions $f, g$ governing the regulatory structure of the underlying two-dimensional system. Constants $\alpha, \beta \in \mathbb{R}$ correspond to degradation rates of $X, Y$, respectively, and when $A = \Delta_G$ is the Laplacian matrix of some graph $G$ this TCFL describes diffusive coupling parameterised by the Turing instability parameter $q$ (the ratio of diffusion coefficients). It was explained in subsection 2.1 that a TCFL can be written as
\[
\dot{x}_i = q^{-1} \frac{\partial H_q}{\partial y_i}, \quad \dot{y}_i = -\frac{\partial H_q}{\partial x_i} + \gamma y_i,
\]
(44)
which is precisely the expression for a deformed conformal Hamiltonian vector field in global symplectic coordinates on $(\mathbb{R}^{2n}, dx_i \wedge dy_i)$. Here the Hamiltonian is $H_q = f(x) - q \alpha y \cdot x + y \cdot A x + q g(y)$ and we have $\gamma = \beta + q \alpha$. Importantly, the part of $H_q$ corresponding to $\hat{H}$ in a decomposition $H_q = H_+ + \hat{H} + q H_-$ is linear in the $y_i$ coordinates, which gives a good indication of what a generalised TCFL should be. The following definition might seem abstract at first, but should quickly be recognised as the correct one once restricted to the case of cotangent bundles.

**Definition 5.** Let $\hat{h} \in TM$ be a vector field satisfying $L_{\hat{h}}(\theta) = 0$ and $H_\pm$ a pair of functions on $M$ satisfying $\partial_\mp H_\pm = 0$. The generalised TCFL associated with the triple $(\hat{h}, H_\pm)$ is the deformed conformal Hamiltonian vector field $X^q_{\gamma,h_q}$ generated by the Hamiltonian
\[
H_q = H_+ + \theta(\hat{h}) + q H_-.
\]
(45)
In general, the functions $H_\pm$ and vector field $\hat{h}$ may also depend on $q$ although this is suppressed in the notation. For cotangent bundles $\pi : T^*B \to B$ we use the definition of the tautological 1-form $\theta(\hat{h})|_z = \langle z, \pi_* \hat{h}(z) \rangle \forall z \in T^*B$ to realise that $\theta(\hat{h})$ is linear along the fibres. In this case $\hat{h}$ can often be identified with the cotangent lift of a vector field $h \in TB$ generating a diffeomorphism of $B$. Then $\theta(\hat{h})$ is just the Hamiltonian generating the symplectomorphism of $(T^*B, \omega)$ coming from the lift of this diffeomorphism. Now that we finally have a definition for generalised TCFLs we are ready to provide some geometric interpretations of their biological characteristics.
To begin with, particularly nice examples of generalised TCFLs arise when the vector field \( \hat{h} \) is a generator for the Hamiltonian action of some Lie group on \((M, \omega)\) with Lie algebra \( \mathfrak{g} \). Then \( \mu(\xi) = \theta(\hat{h}) \) defines a \( \mathfrak{g}^* \)-valued moment map \( \mu : M \to \mathfrak{g}^* \) for the action with \( \xi \in \mathfrak{g} \) the corresponding Lie algebra element. The following examples serve to motivate our study of affine manifolds.

**Example 1.** Let \( B = \mathbb{R}^n \) so that \( M = T^*\mathbb{R}^n \) inherits the Hamiltonian \( GL(n, \mathbb{R}) \)-action lifted from \( B \). We obtain \( \theta(\hat{h}) = y \cdot Ax \) for some \( A \in gl(n, \mathbb{R}) = M(n) \) and the conditions \( \partial_\pm H = 0 \) just say that \( H_+ = f(x) \) and \( H_- = g(y) \). The resulting Hamiltonian is \( H_q = f(x) + y \cdot Ax + qg(y) \) and \( X^q_{0,H_q} \) defines the generalised TCFL

\[ \begin{align*}
\dot{x}_i &= \frac{\partial g(y)}{\partial y_i} + q^{-1} A_{ij} x_j, \\
\dot{y}_i &= -\frac{\partial f(x)}{\partial x_i} - A_{ji} y_j,
\end{align*} \tag{46} \]

which is the TCFL (43) without degradation. If \( A = \Delta_G \) then we have identified the graph \( \mathcal{G} \) with a specific Lie algebra element and similarly can do so whenever \( A \) is a matrix associated with \( \mathcal{G} \).

**Example 2.** Again take \( M = T^*\mathbb{R}^n \) this time with a Hamiltonian \( \mathbb{R}^n \)-action lifted from the action of \( B = \mathbb{R}^n \) on itself by translations. In this case each generator \( b \in \mathbb{R}^n \) gives rise to \( H_q = f(x) + qg(y) \), where we have let \( H_- \) depend on \( q \) and \( b \) in order to cancel out the \( \theta(\hat{h}) = b \cdot y \) term that would otherwise appear in the Hamiltonian. Since \( H_q \) is simple the resulting vector field \( X^q_{\mathcal{G},H_q} \) is an ordinary conformal Hamiltonian vector field and the associated generalised TCFL is

\[ \begin{align*}
\dot{x}_i &= \frac{\partial g(y)}{\partial y_i} - \alpha x_i, \\
\dot{y}_i &= -\frac{\partial f(x)}{\partial x_i} - \beta y_i,
\end{align*} \tag{47} \]

which describes the TCFL (43) on the empty graph (the uncoupled TCFL).

Introducing the \( \mathbb{R}^n \)-action was unnecessarily complicated just to obtain the uncoupled TCFL in Example 2, but doing so illustrates how both examples are unified by the action of the affine group \( \text{Aff}(\mathbb{R}^n) = \mathbb{R}^n \rtimes GL(n, \mathbb{R}) \). Vector fields generating the action of \( \text{Aff}(\mathbb{R}^n) \) on \( \mathbb{R}^n \) take the form \( h = (A_{ij} x_i + b_j) \partial / \partial x_j \) and a Hamiltonian \( H_q = f(x) - q\alpha y \cdot x + y \cdot Ax + qg(y) \) can always be constructed in this way after normalising away unwanted factors, resulting in the TCFL (43). A standard fact is that every compact, complete affine manifold \( B \) arises as a quotient \( B = \mathbb{R}^n / \Gamma \) where \( \Gamma \subset \text{Aff}(\mathbb{R}^n) \) acts properly discontinuously and cocompactly on \( \mathbb{R}^n \). The subgroup of
diffeomorphisms preserving the affine structure of $B$ is given by the quotient $\text{Aff}(B) = N(\Gamma)/\Gamma$ with $N(\Gamma) \subset \text{Aff}(\mathbb{R}^n)$ the normaliser of $\Gamma$ in $\text{Aff}(\mathbb{R}^n)$, and consequently $T^*B$ inherits the action of $N(\Gamma)/\Gamma$ by affine transformations. Identifying $\hat{h}$ with the cotangent lift of a vector field generating this action we find that a generalised TCFL on $T^*B$ takes the form (43) in an affine coordinate chart where $A$ is the linear part of a matrix representation of $\text{Aff}(B)$.

More generally, any affine manifold $B$ comes equipped with a flat connection $D$ that satisfies $D_{\partial/\partial x_i} \partial/\partial x_j = 0$ in each affine coordinate chart $\{x_i\}$. A Riemannian metric $G_B$ on $B$ is called Koszul if there exists a closed 1-form $\eta$ such that $G_B = D\eta$, and hence locally $G_B = DdK$ for some convex function $K : B \to \mathbb{R}$. Affine coordinates and a Koszul metric determine local symplectic coordinates on $T^*B$ in which the standard symplectic form is given by $\omega = dx_i \wedge dy_i$. The Sasaki metric $G$ and almost complex structure $J$ associated with $G_B$ are, in matrix form respectively,

$$G = \begin{pmatrix} G_B & 0 \\ 0 & G_B^{-1} \end{pmatrix}, \quad J = \begin{pmatrix} 0 & -G_B^{-1} \\ G_B & 0 \end{pmatrix},$$

where the condition $G_B = DdK$ implies $(G_B)_{ij} = \partial K/\partial x_i \partial x_j$. From section 3 it follows that $\{dx_i\}$ provides a local basis for $\Omega^{1,0}(M)$ and $\{dy_i\}$ a local basis for $\Omega^{0,1}(M)$, therefore in symplectic coordinates a deformed conformal Hamiltonian vector field locally takes the form (44). In general the cotangent lift of any vector field $h = h_i(x) \partial/\partial x_i \in TB$ (not necessarily the generator of an affine transformation) defines a Hamiltonian $H_q = f(x) + y \cdot h(x) + qg(y)$, and we see that a generalised TCFL may have coupling terms that are nonlinear in the local coordinates $\{x_i\}$. Of course there is no reason why this construction should be restricted to affine manifolds, and we will consider generalised TCFLs on cotangent bundles of arbitrary smooth manifolds in section 5. The reason why affine manifolds are particularly important is because of their relevance to Lagrangian torus fibrations (see below) and the fact that there are many instances when the matrix $A$ can be identified with the linear part of an affine transformation. In these cases the Lie derivative of $\omega$ along the direction of a generalised TCFL is given in symplectic coordinates by

$$L_{X^q_{\alpha,\beta}} (dx_i \wedge dy_i) = [(\alpha + \beta) \delta_{ij} + (1 - q^{-1}) A_{ij}] dx_i \wedge dy_j,$$

which determines a variation of the symplectic form within its cohomology class. When $A$ is empty the variation is conformally symplectic as described in [9], and so for simplicity we consider only the case $\alpha + \beta = 0$. Then when $1 > q > 0$ the symplectic inner product of
two elements in $TM$ expands exponentially, otherwise it contracts for $q > 1$ and $q < 0$. The biological interpretation of a generalised TCFL explains how the size of this variation depends on the Turing instability parameter. Molecules $X, Y$ having very different diffusion coefficients with the same sign will give rise to a contraction in symplectic area, whilst diffusion coefficients of opposite signs (unlikely to arise in practice) can generate both contraction and expansion. On the other hand, the matrix $A$ determines the direction of this variation. Since $A$ encodes the coupling terms in a generalised TCFL, a complex network with higher connectivity will result in a more complicated variation. The combined effect of having a generalised TCFL with complicated diffusion and complex network structure therefore results in a large amount of dissipation as measured by variation of the symplectic form. This assigns a clear geometric interpretation to the biological parameters $q$ and $A$.

Important examples of Lagrangian fibrations that are not cotangent bundles are Lagrangian torus fibrations. For the key ideas behind the classification of Lagrangian torus fibrations the reader is referred to [24, 25]. From the Arnold-Liouville theorem a smooth Lagrangian fibration $\pi : (M, \omega) \to B$ with connected, compact fibres is necessarily a torus fibration over an integral affine manifold $B$ with transition functions in the subgroup $\mathbb{R}^n \times GL(n, \mathbb{Z}) \subset Aff(\mathbb{R}^n)$. The integral affine structure determines a subbundle $\Lambda^* \subset T^*B$ of integral 1-forms and the holonomy of $\Lambda^*$ is called the affine monodromy of the Lagrangian torus fibration. The fibration $\pi : M \to B$ is a principal torus bundle if and only if the affine monodromy is trivial and globally there exists an isomorphism $M \cong T^*B/\Lambda^*$ if and only if $\pi : M \to B$ admits a global section. Generalised TCFLs can be defined on exact Lagrangian torus fibrations as before using any vector field $\hat{h} \in TM$ satisfying $L_{\hat{h}}(\theta) = 0$. Given the prevalence of special Lagrangian torus fibrations in the SYZ mirror conjecture [26] it is worth describing how these generalised TCFLs fit into the constructions of semi-flat mirror symmetry [27], and for this reason we work locally where $M \cong T^*B/\Lambda^*$. This assigns further geometric meaning to the Turing instability parameter. In symplectic coordinates the metric $G_q$ is

$$G_q = (G_B)_{ij}dx_i \otimes dx_j + q(G_B^{-1})_{ij}dy_i \otimes dy_j \quad (50)$$

and we find that the diameter of $M$ stays bounded whilst the volume of the fibres shrink to zero as $q \to 0$. Translating this to the family of almost complex structures $\{J_q\}$ we recognise the limit $q \to 0$ as the large complex structure limit of mirror symmetry (see [27, 28] and references
therein). Thus, as suggested in subsection 2.1, one may assign a geometric interpretation to the biological limit where one diffusion coefficient becomes very large compared to the other. We defer the geometric interpretation of the complimentary limit, \( q \to -1 \), to the next subsection.

Since a generalised TCFL can be identified with a variation of the symplectic form within its cohomology class, the mirror dual of generalised TCFL is simply a variation of the complex structure on the mirror manifold \( M' \). Let us briefly explain this statement following [27]. The flat connection \( D \) and metric \( G_B \) together define a dual connection \( D' \) on \( B \) where \( \frac{1}{2}(D + D') \) is the Levi-Civita connection of \( G_B \). Then a change of affine structure to the one determined by \( D' \) combined with fibrewise dualisation locally defines the mirror manifold \( M' \cong TB/\Lambda \), where \( \Lambda \) is the subbundle dual to \( \Lambda^* \). The symplectic form on \( M' \) is given locally by \( \omega' = (G_B)_{ij}dx'_i \wedge dy'_j \) and metric \( G' \) and complex structure \( J' \) are

\[
G' = \begin{pmatrix} G_B & 0 \\ 0 & G_B \end{pmatrix}, \quad J' = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix},
\]

respectively. As described in [27], our choice of coordinates on \( M \) imply that if the symplectic structure \( \omega \) is varied whilst \( J \) remains fixed it is the complex structure \( J' \) that varies on \( M' \) whilst \( \omega' \) remains fixed. A vector field generating the latter could be interpreted as the mirror dual of a generalised TCFL and the hope is that this provides an alternative method for studying these dynamical systems in the future. For this reason it would also be interesting to extend the definition of generalised TCFLs to singular Lagrangian torus fibrations.

4.2. Bi-Lagrangian manifolds and products of Lorentz surfaces

In the previous subsection it was more natural to assume that \( q > 0 \), but from the biological interpretation of a generalised TCFL one expects to have \( q < 0 \). In this case the metric \( G_q \) is no longer Riemannian but instead a pseudo-Riemannian metric with neutral signature. In fact when \( q = -1 \) the metric

\[
G_{-1} = G_B \oplus -G_F
\]

is precisely the standard metric induced by a choice of \textit{almost} \( \mathbb{D} \)-complex structure \( T \) on \( M \) (here we use the terminology of Harvey and Lawson [16] whilst others call \( T \) an \textit{almost bi-Lagrangian}, an \textit{almost para-complex}, or an \textit{almost product structure}). In analogy with the complex case an almost \( \mathbb{D} \)-complex structure \( T \) is an automorphism \( T : TM \to TM \) satisfying \( T^2 = id \) with \( G_{-1}(\cdot, \cdot) = \omega(\cdot, T\cdot) \) the standard pseudo-Riemannian metric associated with \( T \). Any Lagrangian
fibration should in principle admit an almost $\mathbb{D}$-complex structure, but here the specific choice of $T$ is determined by the choice of $J$. In particular, the decomposition (7) of $TM$ induced by $J$ coincides with the eigenspace decomposition of $TM$ induced by $T$. Like $J$, $T$ has an associated Nijenhuis tensor and its vanishing is equivalent to the almost $\mathbb{D}$-complex structure being integrable and $(M, T)$ being $\mathbb{D}$-complex. Integrability of $T$ corresponds to $(M, \omega, J)$ being bi-Lagrangian by our terminology or $(M, \omega, T)$ being $\mathbb{D}$-Kähler by that of of Harvey and Lawson. Many of the standard constructions from Kähler geometry carry over to the $\mathbb{D}$-Kähler case and, just as one describes Kähler manifolds using complex coordinates, it is common to discuss these spaces in terms of $\mathbb{D}$-complex numbers (the two-dimensional algebra $\mathbb{D}$ generated by $1$ and $\tau$ satisfying $\tau^2 = 1$). Notions of $\mathbb{D}$-complex conjugates, $\mathbb{D}$-holomorphic functions, and decompositions of forms and the exterior derivative are defined similarly (see [16] for details). For now we continue in the spirit of the previous subsection and assume that both $J$ and $T$ are integrable. This means that $(M, \omega, J)$ is Kähler and $(M, \omega, T)$ is $\mathbb{D}$-Kähler (equivalently $(M, \omega, J)$ is bi-Lagrangian). By allowing negative values of $q$ the family $\{J_q\}$ extended to the interval $q \in [-1,1]$ traces out a path in the combined space of all $\omega$-compatible ($\mathbb{D}$-)complex structures, the $\mathbb{D}$-complex structures compatible in the sense that $\omega(\cdot, T\cdot)$ is a metric of neutral signature on $M$. This path starts at the $\mathbb{D}$-complex structure $T$ with $q = 1$ and ends at the complex structure $J$ with $q = 1$. However, it must also pass through the singular point at $q = 0$ where the metric $G_q$ degenerates on the fibres of $\pi : (M, \omega) \to B$. As described in subsection 4.1, this point represents a boundary or cusp in the space of compatible complex structures and the limit $q \to 0^+$ is precisely the large complex structure limit of mirror symmetry in which the SYZ conjecture is expected to hold [28]. From the symplectic viewpoint this limit is often called the adiabatic limit [29] and in the next section we shall study the adiabatic limit of generalised TCFLs on cotangent bundles.

From a biological perspective we know that $q$ parameterises generalised TCFLs as the ratio of diffusion coefficients or Turing instability parameter. The endpoints and singularity of the path $\{J_q\}$ therefore correspond geometrically to the biological limits described in subsection 2.1. In particular, when $X$ and $Y$ diffuse at the same rate a generalised TCFL defines a gradient using the standard psuedo-Riemannian metric associated with $T$ (recall Proposition[2]). This provides a concrete geometric interpretation of the biological limit $q \to -1$ and describes how the Turing instability parameter also parameterise the family $\{(M, \omega, J_q)\}$. Allowing $q$ to vary across the
interval \([-1, 1]\) automatically extends semi-flat mirror symmetry to include a duality with \(\mathbb{D}\)-Kähler geometry and it turns out that analogues of special Lagrangian submanifolds (the basis of the SYZ conjecture) have already been studied there [16]. In particular, it is the Ricci-flat, affine \(\mathbb{D}\)-Kähler manifolds that provide the natural duals of Calabi-Yau manifolds and because of their bi-Lagrangian structure these are also Lagrangian torus fibrations over an affine base equipped with Koszul metric. If suitably defined, the parametrisation \(\{J_q\}\) should provide a way to move between Kähler and \(\mathbb{D}\)-Kähler Lagrangian fibrations, perhaps as submanifolds in a higher-dimensional ambient space. Mirror symmetry could then be used to set up a quadrality involving mirror pairs of both types of geometry. It is nice to think that the biological interpretation of TCFLs could motivate the problem of extending mirror symmetry to include such a construction. To the best of our knowledge nothing along these lines has appeared in the literature so far.

Two-dimensional bi-Lagrangian manifolds are necessarily Lorentz surfaces and therefore non-compact if not the torus. Simple higher-dimensional examples can be obtained by taking \(n\)-fold products of these [14], and Lagrangian fibrations of this type form a good starting point for discussing the synchronisation properties of a generalised TCFL. In complex network theory the state \(S = \{(z_1, \ldots, z_n) : z_i = z_j \forall i, j\}\) (with \(z_i = (x_i, y_i)\) in this case) is usually called the synchronised state of a complex network [6, 7, 8], but of course this is only globally well-defined as a submanifold using the existence of global coordinates on \(\mathbb{R}^{2n}\). Generally \(S\) is not well-defined for an arbitrary Lagrangian fibration. However, it is well-defined as the diagonal in \(n\) copies of a Lorentz surface where biologically the product structure reflects the fact that the underlying two-dimensional system on each vertex is identical. From previous examples of generalised TCFLs where the matrix \(A\) was the Laplacian \(\Delta_G\) it follows that a distinguishing feature of \(\theta(\hat{h})\) is that it must vanish on this diagonal. Given this observation we therefore take the submanifold \(S \subset M\), well-defined by the condition that \(\theta(\hat{h}) = 0\) everywhere on \(S\), as the generalised synchronised state of a generalised TCFL with Hamiltonian \(H_q = H_+ + \theta(\hat{h}) + qH_-\). On an arbitrary Lagrangian fibration \(H_q\) restricts to a simple Hamiltonian \((H_+ + qH_-)|_S\) on \(S\), and by Proposition 3 the associated deformed Hamiltonian vector field becomes symplectic. Consequently, what one can say about “synchronisation” for a particular generalised TCFL \(X^{\theta}_{\gamma,H_q}\) of \(S\) one could possibly obtain limit cycle behaviour. The concept of synchronisation in dynamical systems on differentiable manifolds also seems to be new.
5. Adiabatic limits of generalised TCFLs

In this final section we study the behaviour of a generalised TCFL as \( q \to 0 \) to obtain a lower bound on the number of its equilibrium solutions. As described in subsection 2.1, this estimate has important consequences for multistability of the associated biological system \([5, 10]\). The approach is more conjectural than in previous sections since we do not have at our disposal the analytic tools required for an in-depth study of the adiabatic limit. So far we have described two ways in which the limit \( q \to 0 \) is related to our study of deformed Hamiltonian vector fields. The first arises because it has a biological interpretation as the limit where the diffusion coefficient of molecule \( X \) becomes very large compared to that of \( Y \). The second is because from a geometric perspective it describes a singularity in the space of all compatible (\( \mathbb{D} \)-)complex structures. The context in which we shall study the adiabatic limit is related to the discussion at the end of section 3. We consider a Morse-type model for Floer theory with generalised TCFLs and try to obtain a topological estimate for the number of equilibrium solutions, which becomes possible in the adiabatic limit. In particular, we restrict to cotangent bundles \( T^*B \) where we conjecture that this number is bounded below by the Betti numbers of the generalised synchronised state introduced in subsection 4.2. This formalises the intuitive idea that the number of equilibrium solutions of a complex network should be at least as many as in the synchronised state. In section 5.2 we explain how the adiabatic limit construction could be extended to describe the Fukaya category of cotangent bundles.

5.1. Adiabatic chain complex

We shall argue that Morse theory with a generalised TCFL on \( T^*B \) should yield the singular homology of a submanifold \( S \subset T^*B \) that may in turn be identified with the generalised synchronised state of subsection 4.2. In particular, this would imply that the number of equilibrium solutions of the generalised TCFL is bounded below by the sum of the Betti numbers of \( S \). The starting point for obtaining information about \( S \) given data on \( T^*B \) is an extension of the Lagrange multiplier Morse theory developed in \([30, 31]\). Frauenfelder (and Schecter-Xu for the rank one case) considered Morse theory on the trivial vector bundle \( B \times V^* \to B \) using a smooth function \( F : B \times V^* \to \mathbb{R} \) given by

\[
F(x, v^*) = f(x) + v^*(h(x)) ,
\]

(53)
where \( v^* \in V^* \), \( f : B \to \mathbb{R} \) and \( h : B \to V \). Here \( V^* \) is the dual of a finite dimensional vector space \( V \). If 0 is a regular value of \( h \), then it is a well-known fact that there exists a bijective correspondence \( \lambda : \text{Crit}(F) \to \text{Crit}(f|_{h^{-1}(0)}) \) between critical points of \( F \) and critical points of \( f|_{h^{-1}(0)} \). Using several different approaches, both [30] and [31] prove the existence of a homotopy between the moduli spaces of gradient flow lines of \( F \) on \( B \times V^* \) and those of \( f|_{h^{-1}(0)} \) on \( h^{-1}(0) \). Most relevant to us is the adiabatic limit method used in [31] to show that gradient flow lines of \( F \) converge to those of \( f|_{h^{-1}(0)} \) as the volume of the fibre is taken to zero. There are two issues that arise when generalising this result to general Lagrangian fibrations \( \pi : (M, \omega) \to B \).

1) It is natural to take the generalisation of \( h \) to be a section of the dual fibration whose zero locus, \( h^{-1}(0) \), defines the submanifold of interest. The problem is that the concept of a dual fibration and zero locus (in the sense required for the Lagrange multiplier construction) becomes ambiguous in cases where the fibres need not be vector spaces. In particular, for most compact fibres there is no notion of a uniquely distinguished point at 0.

2) In general, \( B \times V^* \) is of rank \( k < n \) so that \( h^{-1}(0) \subset B \) is a submanifold of dimension \( n - k > 0 \). For a Lagrangian fibration the fibres are always of dimension \( n \) however, which means that \( h \) must degenerate on certain fibre directions if we are to ensure \( n - k \) is nonzero. Even if \( f \) is Morse this necessarily implies \( F \) can only ever be Morse-Bott so that something must be done to account for the “left over” directions of the fibration.

The second point is most easily addressed by perturbing \( F \) using a family of Morse functions having compact support on the degenerate directions associated with critical submanifolds. Although \( F \) is Morse-Bott its perturbation becomes Morse [32]. It is precisely this approach that means we can realise \( H_q \) as a perturbed Morse-Bott function with \( q \) interpreted as the small parameter of the perturbation, \( H_- \) the perturbing Morse function, and \( \theta(\hat{h}) \) and \( H_+ \) can be identified with the appropriate generalisations of \( v^*(h(x)) \) and \( f(x) \), respectively. To address the first point we shall content ourselves with considering cotangent bundles \( M = T^*B \) where \( B \) is a closed, oriented manifold that is not necessarily affine. The choice of almost complex structure is again determined by the Sasaki metric \( G \) after a choice of metric \( G_B \) on \( B \).

Our assumption on the vector field \( \hat{h} \) used to construct a generalised TCFL as in Definition
is that its horizontal projection is a vector field \( h : B \to TB \) that has zero set \( h^{-1}(0) \subset B \) with codimension \( k \) as a closed, oriented submanifold of \( B \). We use \( h_i \) to denote the \( n \) functions \( h_i : B \to \mathbb{R} \) defined by \( h \) in an appropriate trivialisation and impose that the vertical projection of \( dh \) has rank \( k \). For simplicity we also restrict to the case \( \gamma = 0 \) so that the generalised TCFL is just defined in terms of the deformed Hamiltonian vector field \( X^q_{H_q} \). The Hamiltonian \( H_q \) is then constructed using a Morse function \( H_+ = f : B \to \mathbb{R} \) together with a function \( H_- = g \) whose domain will include the critical submanifolds of \( H_0 \equiv H_{q=0} \). We assume further that the restriction \( f|_{h^{-1}(0)} \) is a Morse function on \( h^{-1}(0) \) and extending \( g \) to the whole of \( T^*B \) using cut-off functions we obtain the Hamiltonian

\[
H_q(z) = f(\pi(z)) + \langle z, h(\pi(z)) \rangle + qg(z) , \quad q \in (0, 1],
\]

where \( z \in T^*B \) (compare this with Definition 5). To illustrate how \( H_q \) can be viewed as a perturbed Morse-Bott function and define \( g \) properly we shall first consider the critical point set of

\[
H_0(z) = f(\pi(z)) + \langle z, h(\pi(z)) \rangle ,
\]

which is the analogue of \( F \) in [30, 31]. The critical point set of \( H_0 \) consists of pairs \((x, y)\) satisfying (in local coordinates)

\[
h_i(x) = 0 , \quad df(x) + y_i dh_i(x) = 0 ,
\]

which by the assumptions on \( h \) is just the condition that \( x \in h^{-1}(0) \) is a critical point of \( f|_{h^{-1}(0)} \). The combination of the \( y_i \) spanning the vertical kernel of \( dh \) define a \((n-k)\)-dimensional fibre \( Z_x \) over \( x \) that we assume can be extended to a proper fibre bundle \( Z \to h^{-1}(0) \). Because \( f|_{h^{-1}(0)} \) is a Morse function with isolated critical points the critical point set of \( H_0 \) is a disjoint union of isolated critical submanifolds \( V_x \cong Z_x \) that are identified with the fibres of \( Z \) over each critical point \( x \in \text{Crit}(f|_{h^{-1}(0)}) \),

\[
\text{Crit}(H_0) = \coprod_{x \in \text{Crit}(f|_{h^{-1}(0)})} V_x .
\]

This shows that critical submanifolds of \( H_0 \) are in one-to-one correspondence with critical points of \( f|_{h^{-1}(0)} \). Using an argument similar to Frauenfelder [30] we find that \( H_0 \) is Morse-Bott and for indices the following relation holds

\[
\text{index}_{H_0}(V_x) = \text{index}_{f|_{h^{-1}(0)}}(x) + k .
\]
Returning to the case \( q \neq 0 \) it is now straightforward to see that choosing \( g \) to define a family of Morse functions \( g_x : Z_x \to \mathbb{R} \) parameterised by \( x \in h^{-1}(0) \) means that \( H_q \) is a Morse function on \( T^*B \). Critical points \( p \) of \( H_q \) can be identified with pairs \((x, y)\) where \( x \in h^{-1}(0) \) is a critical point of \( f|_{h^{-1}(0)} \) and \( y \) is a critical point of \( g_x \) on the fibre \( Z_x \). The index of a critical point \( p = (x, y) \in \text{Crit}(H_q) \) is

\[
\text{index}_{H_q}(p) = \text{index}_{f|_{h^{-1}(0)}}(x) + \text{index}_{g_x}(y) + k \, ,
\]

and these are equilibrium solutions of the generalised TCFL determined by \( X^q_{H_q} \). We would like to obtain a lower bound on the number of these solutions and for that reason shall introduce a Morse-type complex generated by critical points of \( X^q_{H_q} \). By Proposition 2, for fixed \( q \) we have that \( JX^q_{H_q} \) is the negative gradient of \( H_q \) defined with respect to the metric \( G_q \). Denote by \( \phi^q_t : T^*B \to T^*B \) the flow of

\[
\frac{du}{dt} = JX^q_{H_q}(u) \, ,
\]

and for each \( p \in \text{Crit}(H_q) \) define the stable and unstable manifolds by

\[
W^s_q(p) = \{ z \in T^*B \mid \lim_{t \to +\infty} \phi^q_t(z) = p \} \, , \quad W^u_q(p) = \{ z \in T^*B \mid \lim_{t \to -\infty} \phi^q_t(z) = p \} \, ,
\]

respectively. For \( q \in (0, 1] \) we assume the pair \((H_q, G_q)\) satisfy the Morse-Smale condition so that for all \( p^\pm \in \text{Crit}(H_q) \) the family of moduli spaces

\[
\mathcal{M}_q(p^-, p^+) = W^u_q(p^-) \cap W^s_q(p^+) / \mathbb{R} \, ,
\]

is a family of smooth manifolds all of dimension

\[
\dim(\mathcal{M}_q(p^-, p^+)) = \text{index}_{H_q}(p^-) - \text{index}_{H_q}(p^+) - 1 \, .
\]

Thus, we can define a family of Morse-Smale-Witten complexes, \( \mathcal{C}_*(H_q, J_q) \), by counting flow lines of \( X^q_{H_q} \) that join critical points of \( H_q \). The notation \( \mathcal{C}_*(H_q, J_q) \) indicates the choice of Hamiltonian and almost complex structure. One might hope that, since the generators are identical, it might be possible to relate the differentials of \( \mathcal{C}_*(H_q, J_q) \) with a Morse complex on the total space of \( Z \to h^{-1}(0) \). The problem is that flow lines of \( JX^q_{H_q} \) may be very different to the gradient flow lines of \(-f|_{h^{-1}(0)} + g\) that are required to construct such a Morse complex. In particular, it is certainly not true that flow lines of \( JX^q_{H_q} \) must be constrained to the submanifold \( Z \subset T^*B \). However, as \( q \) goes to zero the only flow lines of \( JX^q_{H_q} \) that contribute to the differential are those
that converge to gradient flow lines on \( Z \) (to prove this rigorously following [31] we would need to appeal to a recent theorem by Eldering [33] on persistence of noncompact normally hyperbolic invariant manifolds). This implies that in the adiabatic limit elements of \( W^u_q(p^-) \cap W^s_q(p^+) \) are in bijection with maps \( u : \mathbb{R} \to Z \) satisfying

\[
\frac{du}{dt} = -\nabla (f|_{h^{-1}(0)} + g)(u), \quad \lim_{t \to \pm \infty} u(t) = p^\pm, \tag{64}
\]

where \( p^\pm \) are the critical points corresponding bijectively to \( (x^\pm, y^\pm) \). Thus, for \( q \) sufficiently small, we obtain an isomorphism of moduli spaces that means we can identify \( C_*(H_q, J_q) \) with a Morse complex on \( Z \).

We call the chain complex obtained from \( C_*(H_q, J_q) \) in this way the \textit{adiabatic chain complex}. By standard arguments for Morse theory on vector bundles over closed, oriented manifolds the homology of the adiabatic chain complex is isomorphic to the singular homology of \( h^{-1}(0) \) with grading shifted down by \( k \). In turn we may identify the singular homology of \( h^{-1}(0) \) with that of the generalised synchronised state \( S \), which is itself a vector bundle over \( h^{-1}(0) \). Thus, for \( q \) sufficiently small, we obtain an isomorphism

\[
H_*(C_*(H_q, J_q)) \cong H_{*-k}(S), \tag{65}
\]

which describes how topological information about a submanifold \( S \subset T^*B \) is encoded by a choice of generalised TCFL. In particular, we obtain a lower bound on the number of equilibrium solutions of the generalised TCFL

\[
\dot{z}(t) = X^{H_q}_q(z(t)), \quad H_q = H_+ + \theta(\hat{h}) + qH_-. \tag{66}
\]

**Conjecture 1.** For sufficiently small \( q \) the number of equilibrium solutions to the generalised TCFL (66) is bounded below by

\[
\sum_{a=0}^{n-k} \dim H_a(S), \tag{67}
\]

where \( S \) is the generalised synchronised state defined by \( \theta(\hat{h}) = 0 \).

This statement must be taken as conjectural since the argument provided above is only the sketch of a mathematical proof. In biological terms it implies that a generalised TCFL must
have at least as many equilibrium solutions as it does in the generalised synchronised state, which is tautological for a TCFL on \( \mathbb{R}^{2n} \) where the synchronised state is just the kernel of the Laplacian \( \Delta_g \). For spaces of non-trivial topology this may not be the case however, and one could easily envisage a situation where Morse theory predicts the minimal number of critical points on a submanifold to be larger than that on the ambient space. This would almost certainly cause a problem when extending the definition of generalised TCFLs to compact manifolds and Conjecture 1 to Lagrangian fibrations other than cotangent bundles. The condition that the diffusion coefficient of molecule \( X \) must be sufficiently large compared to that of \( Y \) (i.e. the Turing parameter must be sufficiently small) could probably be relaxed given an appropriate set of assumptions.

5.2. The Fukaya category of cotangent bundles

We end with some speculatory remarks on using generalised TCFLs to describe the Fukaya category of cotangent bundles. In the previous subsection we argued that to each generalised TCFL on \( T^*B \) there is an associated family of chain complexes, \( \mathcal{C}_n(H_q, J_q) \), which yields the singular homology of the submanifold \( h^{-1}(0) \subset B \) in the adiabatic limit. From the work of Fukaya-Oh [29] we also know that in the adiabatic limit a subcategory of the Fukaya category generated by Lagrangian sections of \( T^*B \) degenerates into a Morse category on \( B \). In this subsection we discuss how these two concepts are related and suggest that generalised TCFLs describe a “complimentary” subcategory of the Fukaya category of \( T^*B \). The Fukaya category of a symplectic manifold \((M, \omega)\) is an \( A_\infty \)-category whose objects are Lagrangain submanifolds \( L \subset M \) and morphisms between the pair of objects \( L_0, L_1 \) are the Floer cochain groups \( CF^*(L_0, L_1) \) introduced in subsection 2.2. Conventions for \( A_\infty \)-categories are taken from [34]. In particular, for \( \mathcal{A} \) a non-unital \( A_\infty \)-category (where non-unital implies not necessarily unital) consisting of \( \mathbb{Z} \)-graded vector spaces \( \text{Hom}_{\mathcal{A}}(A_i, A_j) \) for all objects \( A_i, A_j \in \text{Ob}(\mathcal{A}) \), there exist composition maps \( \text{Hom}_{\mathcal{A}}(A_{id-1}, A_{id}) \otimes \cdots \otimes \text{Hom}_{\mathcal{A}}(A_{i_0}, A_{i_1}) \rightarrow \text{Hom}_{\mathcal{A}}(A_{i_0}, A_{i_d})[2-d], d \geq 1 \). The condition for \( \mathcal{A} \) to be an \( A_\infty \)-category is that these composition maps must satisfy the \( A_\infty \)-associativity equations given in Chapter 1 of [34]. One can associate to \( \mathcal{A} \) its cohomological category \( H(\mathcal{A}) \) that has the same objects as \( \mathcal{A} \) with morphisms the cohomology groups \( H_*(\text{Hom}_{\mathcal{A}}(A_i, A_j), \mu^1_{\mathcal{A}}) \), and composition defined by \([a_i] \cdot [a_j] = (-1)^{\text{deg}(a_i)}[\mu^2_{\mathcal{A}}(a_i, a_j)]\). When \( \mathcal{A} \) is unital, \( H(\mathcal{A}) \) is an honest \( \mathbb{Z} \)-graded linear category. Likewise, if \( \mu^d_{\mathcal{A}} = 0 \) for all \( d > 2 \) then \( \mathcal{A} \) is called a non-unital
differential graded category (dg-category).

One problem with describing the Fukaya category of cotangent bundles $T^*B$ is that there are several possible ways of treating noncompact Lagrangians and it is a little unclear which of these to choose (options are reviewed in [35]). Failure to specify a choice leaves the definition of the Fukaya category ambiguous. Perhaps most relevant to us is the approach of Nadler and Zaslow [36] where one interprets Lagrangian submanifolds of $T^*B$ as constructible sheaves on $B$. In this version of the Fukaya category, $\mathcal{F}(T^*B)$, objects are formal sums

$$L_{N,F} = \nu^*N + \Gamma_{dF} \subset T^*B,$$

where $\nu^*N$ is the conormal bundle of a closed, oriented submanifold $N \subset B$ and $\Gamma_{dF}$ is the graph of the differential of a function $F : B \rightarrow \mathbb{R}$, i.e. an exact Lagrangian section. Fukaya and Oh [29] have shown that the full subcategory generated by Lagrangian sections is $A_\infty$-equivalent (see [34] for the definition of when two $A_\infty$-categories are $A_\infty$-equivalent) to a Morse category on $B$ and so it is natural to ask whether a similar construction exists for the conormal bundles. This question has been considered by Blumberg, Cohen and Teleman [37] who conjectured that the full subcategory $\mathcal{F}_{conor}(T^*B)$ generated by conormal bundles of closed, connected, submanifolds of $B$ is $A_\infty$-equivalent to the string topology category generated by these submanifolds. Details of the string topology category will not concern us here except to remark that their conjecture was based on the observation that the Floer cohomology $HF^*(\nu^*N_0, \nu^*N_1)$ is isomorphic to the cohomology of paths connecting submanifolds $N_0, N_1 \subset B$. In particular, if the pair $N_0, N_1$ have connected, transverse intersection, $N_0 \cap N_1$, it follows that

$$HF^*(\nu^*N_0, \nu^*N_1) \cong H^{*-\text{codim}(N_0)}(N_0 \cap N_1)$$

(see example 2.2 in [35]).

Returning to the setting of subsection 5.1, suppose one is given a pair of generalised TCFLs on $T^*B$ whose adiabatic chain complexes compute the singular homology of submanifolds $N_0$ and $N_1$, respectively. Moreover, assume that we can define a third generalised TCFL whose adiabatic chain complex yields the singular homology of the transverse intersection $N_0 \cap N_1$. The condition for being able to do so is just that submanifolds $N_{i,j} \equiv N_i \cap N_j$ can each be identified with the zero locus of vector fields $h_{i,j} : B \rightarrow TB$ ($i, j \in \{0, 1\}$). We use $H_{q}^{i,j}$ to denote the Hamiltonian constructed with the vector field $h_{i,j} : B \rightarrow TB$

$$H_{q}^{i,j}(z) = f(\pi(z)) + \langle z, h_{i,j}(\pi(z)) \rangle + qg(z),$$

(70)
so that from (69) the adiabatic chain complex of $C_\ast(H_{q}^{i,j}, J_q)$ can be used to compute the Floer cohomology $HF^\ast(\nu^*N_i, \nu^*N_j)$. Following the logic of Blumberg, Cohen and Teleman, one could also try to define compositions in terms of generalised TCFLs to construct an $A_\infty$-category whose morphism spaces correspond to these chain complexes. Then, as a corollary of their conjecture there should exist an $A_\infty$-equivalence between this category and the subcategory of $\mathcal{F}_{conor}(T^*B)$ generated by $\nu^*N_0, \nu^*N_1 \subset T^*B$.

As a first step towards this construction we note that most of the appropriate tools have already been provided by Abouzaid in [38]. Abouzaid introduced a Morse category, $\mathcal{S}(B)$, generated by the pair $N_0, N_1 \subset B$ with morphism spaces $CM^\ast(N_{i,j})$ (Morse cochains on $N_{i,j}$) and compositions $CM^\ast(N_{id-1,iq}) \otimes \cdots \otimes CM^\ast(N_{i0,i1}) \to CM^\ast(N_{i0,iq})[2-d], d \geq 1$. These compositions were defined using moduli spaces of perturbed gradient flow trees for which we assume there correspond trees of generalised TCFLs that behave just like generalised TCFLs in the adiabatic limit. Then all the ingredients for compositions could be obtained from trees of generalised TCFLs in the limit $q \to 0$. Precise details are well beyond the scope of this paper, but Abouzaid has been able to prove that $\mathcal{S}(B)$ is $A_\infty$-equivalent to the full subcategory of $\mathcal{F}_{conor}(T^*B)$ generated by the pair $\nu^*N_0, \nu^*N_1$. This proves the special case of the Blumberg, Cohen and Teleman conjecture that is required to describe this part of the Fukaya category in terms of generalised TCFLs. Of course, such a description relies on first verifying the arguments outlined in subsection 5.1 for convergence of flow lines as well as trees, but once this has been achieved many other categorical aspects of symplectic geometry may also find a role for generalised TCFLs.

6. Concluding remarks

This paper grew out of an attempt to find a place for TCFLs in the setting of symplectic geometry and bring a selection of ideas from biology to the wider mathematical community. In doing so we have found that many of the biological features characterising a generalised TCFL are naturally described by the structure of Lagrangian fibrations, which provides a new perspective on standard constructions in the field. The fact that these dynamical systems are well-suited to symplectic geometry should come as no surprise given their definition in terms of deformed Hamiltonian vector fields, but it is particularly nice to see that their biological interpretation has also motivated several mathematical problems that do not seem to have appeared in the literature so far. Amongst them is the possibility of a deformed symplectomorphism group, an
extension of mirror symmetry to $\mathbb{D}$-Kähler manifolds, and the idea of Floer theory with deformed Hamiltonian vector fields. In addition, many of the questions that might usually be asked by a mathematical biologist studying TCFLs or other complex networks have been translated into the topological setting. For example, the problem of enumerating equilibrium solutions of a generalised TCFL has motivated Morse theory with Lagrange multipliers on cotangent bundles and synchronisation in complex networks has been extended to differentiable manifolds. It is hoped that these sorts of ideas will bring generalised TCFLs and deformed Hamiltonian vector fields to the attention of many researchers working in differential geometry and mathematical physics.

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